ASPECTS OF COMPARATIVE VEGETATIVE MORPHOLOGY AS AN AID TO *ACTINIDIA* TAXONOMY

A thesis submitted in partial
fulfilment of the requirements for the
degree of Doctor of Philosophy in
Plant and Microbial Sciences
in the
University of Canterbury

by

James M. Condon

University of Canterbury
1991

ABSTRACT

This study explores the practical value of comparative morphology as an aid to *Actinidia* taxonomy, using vegetative characters derived from spring and summer shoots of 20-30 taxa, selected from the "NZ D.S.I.R. *Actinidia* germplasm collection" at Auckland and Te Puke during 1988-1989. Data are collected from field-based observations and from samples processed for light and electron microscopy; these are supplemented with observations derived from herbarium specimens collected in China. The taxonomic potential of characters is further tested using multivariate and other statistical methods.

Actinidia are morphologically variable vines which, nevertheless, express genetically-determined form in: their manner of climbing, the types and growth characteristics of shoots and in the ontogenetic expression of shoot form. There is however a strong "opportunistic component" in the realisation of plant form. Some more conservative characters include leaf venation pattern, trichome morphology, arrangement of sclerenchyma fibres and the complement of ergastic crystals associated with vascular bundles of the leaf. Microscopic examination of abaxial foliar trichomes, currently used to demarcate sections of the genus, reveal branched hair types in *Maculatae* and *Strigosae*, which are supposed to be absent (Dunn 1911, Liang 1984) from these sections of the genus. Re-examination of these groups and the characters delimiting them is recommended.

Comparative morphological studies of *Actinidia* in the germplasm collection show that many of the characters of winter-dormant shoots are genotypic in nature. Vines of *Leiocarpae* and *Stellatae* may be identified below the species level by their bud-form characteristics. Discriminant analysis shows the value of bud height and ostiole size in separating major taxonomic and geographic groups. Detailed analysis of bud characters is justified as poor or uneven budbreak currently limits the productivity of commercial cultivars.

Taxonomists need to be more aware of the spatial and temporal potential afforded by vegetative morphological characters in this genus.

The discovery of "water-excreting glands" (= hydathodes) in all *Actinidia* seen, culminating in a combination of "water spending" characters in *A. deliciosa*, has important implications for water-relations in these plants. Hydathodes in *A. deliciosa* are well supplied by craspedodromous venation and the ultimate tracheids terminate in a spatially diffuse but metabolically active environment, in the apices of these glands. The fate and functioning of hydathodes in *Actinidia* needs further research.

The results from this exploratory study are intended to contribute to the programme of genetic and taxonomic studies of *Actinidia*; currently being undertaken by D.S.I.R. Fruit and Trees, Auckland.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

LIST OF PERSONAL COMMUNICATIONS

1. Ferguson, A.R. (Dr),
D.S.I.R. Fruit and Trees,
Mt Albert Research Centre,
D.S.I.R.,
AUCKLAND.

2. Morley-Bunker, M. (Mr),
Department of Horticulture, Parks and Recreation,
Lincoln University,
CHRISTCHURCH.

3. Breitwieser, I. (Dr)
Department of Plant and Microbial Sciences,
Canterbury University,
CHRISTCHURCH.

4. Fineran, B.A. (Dr),
Department of Plant and Microbial Sciences,
Canterbury University,
CHRISTCHURCH.

LIST OF APPENDICES

CHAPTER ONE

INTRODUCTION

This chapter is a general introduction to aspects of the taxonomy, domestication and morphology of *Actinidia*.

1.1 THE KIWIFRUIT INDUSTRY

Kiwifruit is an important horticultural crop developed in New Zealand in recent years and is now also being established in other countries. Current world production of the crop is estimated at 0.53 million tonnes with 0.3 million tonnes of this being produced in N.Z. (Warrington 1990). Export revenue from kiwifruit production in N.Z. in 1988 was $450 million[1]. Kiwifruit berries are prized for their attractive colour, flavour and high nutritional qualities and their longevity in storage and shipping. The kiwifruit industry is based largely on the vegetative propagation of a single female cultivar 'Hayward', selected by Hayward Wright in 1930, and derived in the first instance from a single importation of Chinese seed in 1904. Domestication of the crop and its history has been reviewed by Ferguson and Bollard (1990) and Yerex and Haines (1983).

1.2 *ACTINIDIA* IN TAXONOMY AND HORTICULTURE

The kiwifruit [= *A. deliciosa* var. *deliciosa* cv. Hayward] represents only one cultivar of one species of the 50 or so species in the genus *Actinidia*. *A. deliciosa* now recognised as a separate species (Liang and Ferguson 1984, 1986) was formerly considered to be a variety of the polymorphic species *A. chinensis*. It differs from the latter however, in having "stiff hairs", more elongate fruit and a higher chromosome number (McNeilage and Considine 1989). *A. deliciosa* is a hexaploid (2n = 6x = 174), whereas, *A. chinensis* is a diploid (2n = 2x = 58). Both of these species provide a limited indication of the range of fruit forms found within the genus.

The number of fruits per inflorescence varies from 1-3 in cv. Hayward, which is consistent with the "reduced form" of this pseudodichasial inflorescence. Some taxa such as *A. latifolia* may have up to 20-30 flowers per inflorescence (Plate 1.1D).

---

[1]Source p.464 *New Zealand Official Yearbook* 1990 94th (Ed.), Dept.of Statistics

Fruit shape in the genus may be spherical (e.g. *A. chinensis* var. *chinensis*, Plate 1.1E and *A. eriantha* Plate 1.1B) or ovoid (e.g. *A. chrysantha* (Plate 1.1A) *A. deliciosa* cv. Bruno, Plate 1.1C). The shape of the fruit contributes to its aesthetic appeal, ease of packing and mechanical processing, e.g. canning. The familiar fruit of 'Hayward' is shown in Plate 1.1F.

1.3 *ACTINIDIA* TAXONOMY - PAST AND PRESENT

Lindley (1836) defined the genus *Actinidia* on the basis of plants with a climbing habit and flowers with radiating styles. [*Actinidia* from the Greek word *aktis* meaning ray].

Siebold and Zuccarini (1843) assigned five climbing species from Japan to the Ternstromiaceae and gave them the generic name *Trichostigma.*

Planchon (1847) described *A. chinensis* from one of Fortune's specimens collected in China and reunited *Actinidia* and *Trichostigma* under the genus *Actinidia* which had priority of nomenclature.

Gilg (1893) emphasised the number of flowers per cyme when he subdivided the group into single *(Monanthae)* and many-flowered *(Pleianthae)* types. Dunn (1911) perceived the group as a series of geographically differentiated subunits, which he separated on the basis of abundance of shoot hairs, ovary shape and the presence or absence of lenticels (= "spots"). Li (1952) subdivided Dunn's groups using the morphology complexity of foliar trichomes on the underside of the leaf. Section *Stellatae* were characterised by stellate abaxial hairs, whereas, all other sections of the genus had simple abaxial hairs. Liang (1984) extended the work of Li and he recognised many new taxa below the species level. He subdivided the *Leiocarpae* into two series based on the solidity or lamellation of the pith; the *Stellatae* were also subdivided into series based on the persistence, morphological consistency and complexity of the stellate hairs. The taxonomic history of the genus is summarised in Table 1.1.

The current taxonomic revision of Actinidia by Liang Chou-Fen (1984) contains *ca.* 50 species and as many infraspecific taxa. *Actinidia* are differentiated from related genera by their lianoid habit, dioecy and flowers with numerous styles. Seeds of *Actinidia* are non-arillate with copious quantities of albumen (Dunn 1911).

Species are diagnosed by Liang on the basis of flower colour, leaf shape and dimensions of fruit, leaves and petioles. Varieties are often erected on the basis of minor differences in leaf colour and in the distribution and abundance of trichomes. Identification is often difficult due to the impermanence of some

Fruit of selected *Actinidia* taxa.

PLATE 1.1

A Single ovoid, spotted (= lenticellate) fruit of *A. chrysantha* (*Maculatae*).

B Single ovoid, furry fruit of *A. eriantha* (*Stellatae*).

C Single elongate, hispid fruit of *A. deliciosa* var. *deliciosa* cv. Bruno (*Stellatae*).

D Single infructescence comprising ten glaucous fruit of *A. latifolia* (*Stellatae*).

E Single spherical fruit (hairs caducous) of *A. chinensis* var. *chinensis* (= soft-haired mihoutao) (*Stellatae*).

F Single elongate fruit (hairs persistent; hispid) of *A. deliciosa* var. *deliciosa* cv. Hayward (= stiff-haired mihoutao, the cultivar term 'kiwifruit') (*Stellatae*).

Bar scale = 10 mm

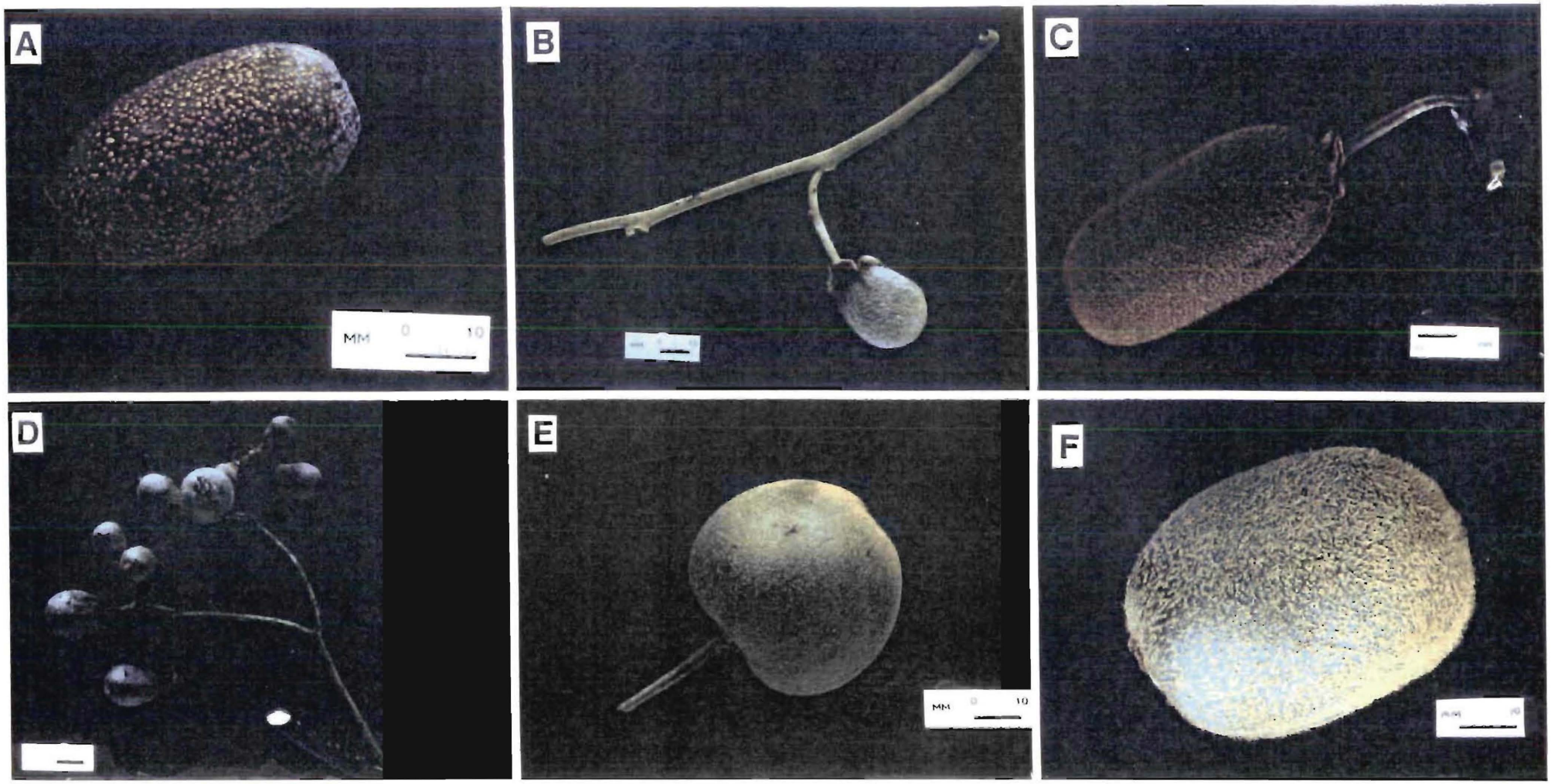
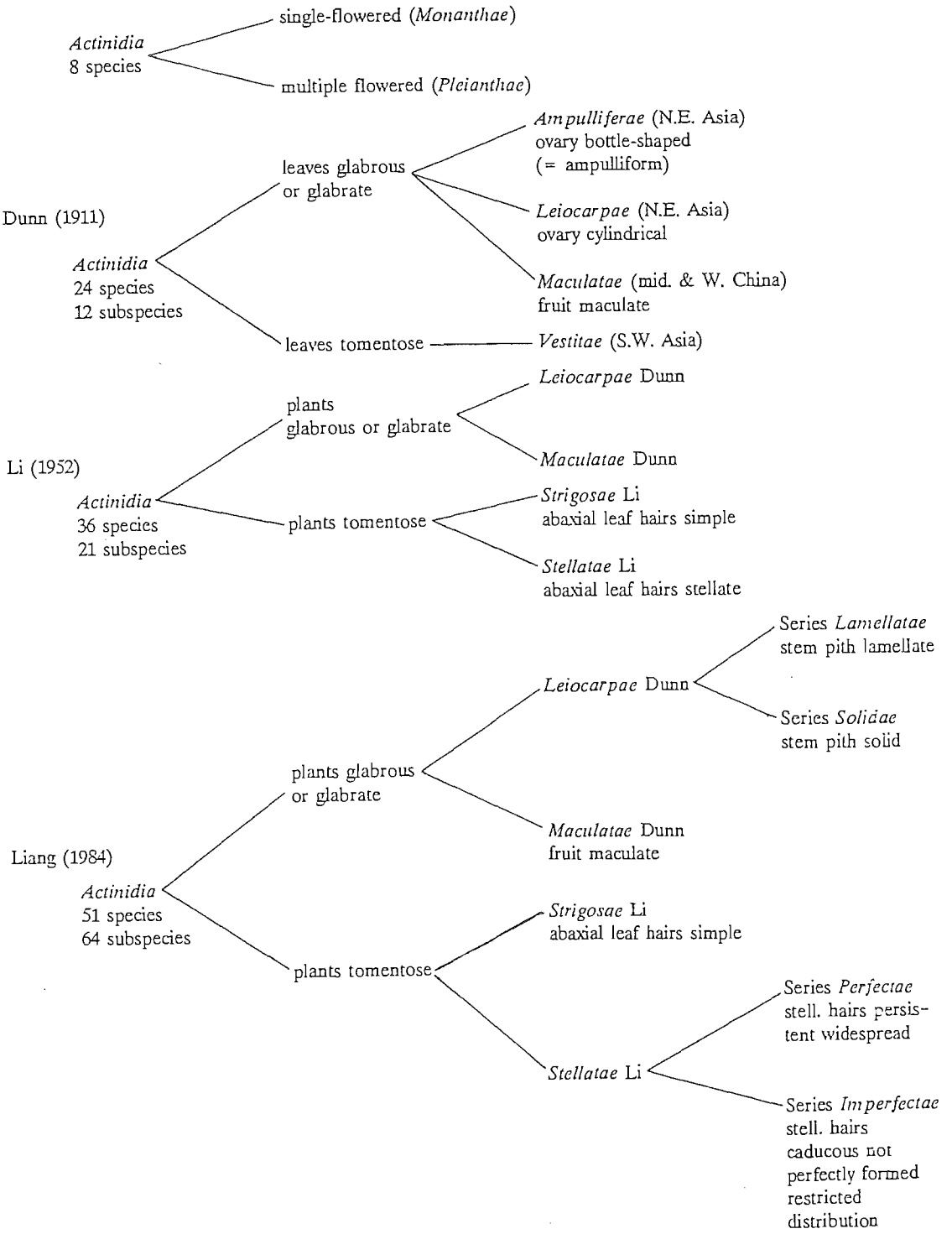

A
MM 0 10
B
C
D
E
MM 0 10
F

Table 1.1 Gilg (1893) **History of *Actinidia* taxonomy**



characters such as caducous hairs, or indeed vegetative and floral characters themselves, since most *Actinidia* are deciduous plants. The identification of winter plants and some hybridising forms is problematical, particularly among widespread polymorphic taxa such as *A. arguta*, which may still be in the process of actively evolving.

For the time being, I accept the composition of the Actinidiaceae as defined by Liang (1984). I am not able to comment on this as I have not examined other genera, e.g. *Clematoclethra*, *Saurauia* or *Sladenia*. It should be noted however that the composition of this family is systematically contentious. Importance has been attached to the following characters in *Actinidia* and related genera: plant habit, presence of raphides, number, arrangement and degree of fusion of floral parts, pattern of embryonic development, number of integuments and the presence of arils.

1.4 HORTICULTURAL POTENTIAL OF SOME *ACTINIDIA* SPECIES

The genus *Actinidia* is centred in the mountains of S.W. China between the Pearl and Yang-tze rivers, where the greatest diversity of taxa occurs (Liang 1983). The ecological range of *Actinidia* is considerable with some taxa extending as far north as Manchuria and others as far south as Indonesia.

Other species besides *A. deliciosa* and *A. chinensis* offer potential for improvement of the crop. Some taxa have very high levels of vitamin C (e.g. *A. eriantha*, *A. latifolia*); others have very different coloured fruits (e.g. red-fleshed *A. arguta* x *A. melanandra*, Seal and McNeilage 1988), or fruits with superior flavour qualities (e.g. *A. chinensis*). Some taxa produce hairless fruit (e.g. *A. arguta* var. *arguta*; *A. chrysantha*), while the fruit of others, (e.g. *A. chinensis*) matures earlier than that of existing cultivars, (e.g. Hayward). The ecological range of *Actinidia* cultivars might be extended by hybridisation with: cold-tolerant Siberian species (e.g. *A. kolomikta*), or with tropical plants (e.g. *A. latifolia; A. indochinensis*). Mindful of this potential for improving kiwifruit, the D.S.I.R. established an *Actinidia* germplasm collection in 1971 (Ferguson pers. comm.).

1.5 REPRODUCTIVE BOTANY OF *ACTINIDIA*

The Actinidiaceae are identified by their conspicuous pistillate (unisexual) flowers with radiating styles. Flowers typically form pseudodichasia borne on long pedicels, emerging from 1 year old canes on 2 yr old wood. Kiwifruit plants are dioecious; consequently adjacent plants of male and female plants are needed to

ensure adequate fruit set in the orchard (Sale 1985). Efforts are being directed toward the development of fruiting males (Ferguson pers. comm.) as dioecy is not absolute in this genus. A well-managed kiwifruit vine in a commercial orchard may produce 1500-2000 fruit, equivalent to a yield of 25 tonnes per hectare (Ferguson and Davison 1986). The development of artificial spray-pollination has resulted in substantial improvements in fruit-set (Hopping 1985). The fruit is harvested when ripe once it has attained a level of 6.2% soluble solids (Harman 1981). The fruit of *A. deliciosa* cv. Hayward is a large, sweet many-seeded berry with a brown hairy exocarp and a fleshy green pericarp.

Reproductive anatomy is documented in several *Actinidia* sp and is reviewed in Ferguson (1984).

Vijayaraghavan (1965) describes the development of the anther. Sporogenous tissues originate from divisions of archesporial mother cells beneath Young anthers have two plates of hypodermal, multicelled archesporial tissue. The central layer of cells becomes sterile in each plate, so that 4 layers of archesporial cells remain. Each plate divides periclinally producing parietal and archesporial cells, respectively. Parietal tissues undergo further cell divisions producing epidermal, endothecial, middle and tapetal layers. Only the epidermal and endothecial cells persist; the middle and tapetal layers eventually degenerate and come absorbed. Microspore mother cells undergo meiosis, during which the cell walls round off and become enclosed by a gelatinous wall. Microspore mother cells undergo cytokinesis simultaneously and their cell walls differentiate into a thick exine and thin intine layer. Division of the microspore nucleus produces a large generative and a small vegetative nucleus and pollen grains are released at the 2-celled stage. In pistillate flowers the microspore nucleus does not divide, the protoplast degenerates and the anther dehisces. In staminate vines the microspore nucleus undergoes normal cell division producing a large vegetative cell and a small generative cell. Pollen of staminate vines is tricolpate with crassimarginate colpi and the grains are prolate to prolate spheroidal in form. Pollen grains are binucleate (Lechner 1915, Schmid 1978) and the pollen is shed in dry clumps (Palmer-Jones and Clinch 1975). According to Corbet *et al.* (1988), *Actinidia* anthers dehisce at the resonant frequency at which bees "buzz". Fertilisation and pollen tube growth in *Actinidia* are described by Harvey *et al.* (1987).

Ovules are axile, anatropous, unitegmic and tenuinucellate (Van Tieghem 1899, Lechner 1915, Vijayaraghavan 1965, Harvey and Fraser 1988). All but one of the megaspores degenerates to form the archesporium (An *et al.* 1983, Harvey and Fraser 1988). Mitosis in the embryo sac is of the *Polygonum* type (An *loc. cit.*).

According to Harvey and Fraser (1988), the polar nuclei fuse to form a uninucleate cell. However, it is generally held (e.g. Esau 1976) that the triploid state of the endosperm in angiosperms originates in one of two ways: either by fusion of one of the sperm nuclei with two haploid nuclei, or by fusion of a single sperm nucleus with a diploid "secondary" nucleus (e.g. Esau 1976). Vijayaraghavan (1965) indicates that the two polar nuclei in *A. polygama* fuse to form a secondary nucleus, but the author does not specify the ploidy of the latter. Further work is needed to clarify the details of endosperm formation in *Actinidia*. Harvey and Freaser *loc. cit.* further note that the primary endosperm nucleus begins to divided 96-180 hrs after fertilisation in *A. deliciosa* and *A. chinensis*. The zygote divides 8 wks after fertilisation and develops through the globular to the heart-shaped stage 12 wks after fertilisation. The embryo is fully formed 16 wks after fertilisation.

The general phenology of *Actinidia* from budbreak to fruiting is summarised on page 8.

Phenology of *A. deliciosa* var. *deliciosa* 'Hayward'

Adapted from Brundell (1975b); Ferguson and Davison (1986)

Shoot Bud Development		Flower Bud Development	New Zealand Calendar
bud dormant	(DAYS)	undifferentiated primordium	January to September
bud swell	-10	formation of floral primordia	
bud-burst	0		late September to October
open cluster	10	initiation of carpels	
		formation of gynoecial plateau	November
	20		
	30	anther and filament initiation	December
	40	ovule initiation	
	50	calyx split	
	60	FULL BLOOM	January

- New buds are thought to be initiated at time of bud-burst.
- Harvest is done between Feb-June, with peak period being May, subject to regional variations in climate.

1.6 VEGETATIVE STRUCTURE IN *ACTINIDIA*

Aspects of the morphology of *Actinidia* have been described in the course of taxonomic revisions of the genus (e.g. Dunn 1911, Li 1952, Liang 1984). These authors have noted the morphological plasticity and variability of vegetative organs in these plants. Whereas the reproductive biology of *Actinidia* has been well-researched (e.g. Anon 1979, Brundell 1975b, Corbet *et al.* 1988, Harvey *et al.* 1987, Harvey and Fraser 1988, Liang 1984, Schmidt 1978, White 1986 a,b) vegetative structures have received much less attention.

There have been some morphological descriptions of buds (Brothers 1988, Brundell 1975a, Lionakis and Schwabe 1984a), internodes (Brundell *loc. cit.* Ferguson 1984, 1990e) and the root systems of the vine (Clothier *et al.* 1986, 1988, Lemon 1988), but these have referred to *A. deliciosa*. Recent observations by Gui (1981), Ferguson (1984, 1990e) and Zhang and Thorp (1986), indicate that vegetative characters might be used to identify *Actinidia* from winter-dormant shoots, given the perennial deciduous nature of most of these vines.

Anatomical studies of stems have largely been exploratory and these have been confined to only a few species, i.e. *A. polygama; A. deliciosa* (e.g. Hitzemann 1886, Metcalfe and Chalk 1950). The size and distribution of vessels in kiwifruit stems have been examined in relation to water transport (McAneney and Judd 1983).

Work on leaf anatomy has been more extensive and here the systematic studies of Lechner (1915), Gao (1988) are discussed in Chapter Two.

The physiological responsiveness of plant form to light quality and quantity was assessed by Morgan *et al.* (1985) in *A. deliciosa*. Low red: far-red light (= simulated shade) increased petiole elongation, but vegetative growth was not markedly affected. Low-light quantity (= low PPFD) did not reduce floral initiation, but development of floral primordia was severely diminished, particularly when the daily integral of PPFD (= photosynthetic photon flux density) was less than or equal to 30% of the incident radiation. Seedlings were shown to be more light-sensitive than adult vines of *A. deliciosa* (Zhu 1983). *Actinidia* behaved as as a warm-temperate plant with increased biomass accumulation under "long-day" conditions. Shoot tips showed increased twisting under "short-days" and petioles were unexpectedly succulent (Lionakis and Schwabe 1984b). *Actinidia* vines grew rapidly in response to water (Ferguson 1984, Lees 1982) and high humidity (Liao and Wang 1984), but growth and fruiting declined markedly in response to wind-damage (McAneney *et al.* 1984).

Actinidia in the wild are straggly, rambling or climbing vines forming impenetrable thickets on occasion. They prefer well-lit humid and sheltered conditions and are often found on margins of forests or near the banks of streams (Kolbasina 1963).

Kiwifruit vines are established as grafted plants in sheltered and intensively managed orchards. They are arranged in an orderly manner on T-bar or pergola frames (Sale 1985), where a permanent trunk supports a perpendicular pair of "leader" branches. The crop is raised 1-2 m above the ground on fruiting arms, which emerge from these leaders at regularly spaced intervals. Fruiting arms consist of 2 yr old stems termed canes, which are pruned in the winter, leaving only the basal 5-10 internodes. The following spring flowers are borne in the axils of the current season's shoots, which arise from buds on the fruiting arms. Summer pruning is used to control excessive vigour of shoots and to increase the penetration of light for photosynthesis and flowering. Vines are pruned (in winter) after flowering, when new fruiting arms are tied down for the next season and arms which have flowered are removed. Under a system of replacement pruning, fruiting arms are renewed every 2-3 years.

Actinidia vines in the germplasm collection are all grown under common conditions in an "experimental garden" (Clausen, Keck and Hiesey 1940) and plants are managed as if they were commercial kiwifruit vines. Thus genotypic variation emerges in a horticultural context.

1.7 DEVELOPMENT OF TOPIC

The thesis began in 1987 with the aim to explore stem structure in relation to transport, with reference to *A. deliciosa* var. *deliciosa* cv. Hayward. Results of some of this work were presented at the 1991 Kiwifruit symposium (see Appendix 5 for conference abstracts). Further examination of plants in the D.S.I.R. germplasm collection and the literature, however, revealed that little was known of the basic morphology of many of these plants. Emphasis was therefore redirected (in July 1988) in studying the taxonomic potential of vegetative morphology in some *Actinidia*. Given the difficulty of obtaining plant material from China, attention was directed towards those taxa of economic potential, currently grown in the N.Z. D.S.I.R. *Actinidia* germplasm collection.

1.8 AIMS OF INVESTIGATION

The aims of this thesis are as follows :

(1) To evaluate the genetic and environmental components of plant form in summer shoots in *Actinidia* vines, in relation to taxonomy;

(2) Detailed study of the taxonomic potential of morphological characters displayed by winter-dormant shoots with some assessment of infraspecific variation in *A. chinensis* and *A. deliciosa*;

(3) Exploratory structural observations of the "water-excreting" glands (= hydathodes) in *A. deliciosa* var. *deliciosa* cv. Hayward, with consideration of their possible mode of operation.

The potential application of this structural information is investigated by comparative (qualitative) and statistical methods and directions for future investigations are indicated.

ADDENDUM CHAPTER ONE : NAME CHANGES

Since completing the final draft of this thesis, Dr A.R. Ferguson (pers. comm.) of D.S.I.R. Fruit and Trees has reassessed the nomenclature of some *Actinidia* in the germplasm collection.

1. *A. arguta* complex

A.R.F. thinks that the N.Z. examples of *A. arguta* var. *arguta* and *A. arguta* var. *cordifolia* represent two morphological extremes within a highly variable group. He is not able to support Liang's (1984) separation of these varieties on morphological grounds, even after examination of Chinese herbarium specimens at Guilin. Further cytotaxonomic and chemical data are thus needed to settle the issue.

2. *A. arguta* var. *giraldii* (4/1/4)

This plant differs from *A. arguta* var. *arguta* in having glaucous leaf undersides and a diploid, rather than tetraploid genome. According to A.R.F., the petioles and leaf undersides are less "hairy" than suggested in descriptions of this plant by Diels and Liang.

Our "*A. giraldii*" plant may be *A. hypoleuca* Nakai. A.R.F. had previously overlooked this species; it is confined to southern and central Japan and is therefore absent from Liang's (1984) descriptions of *Actinidia*. Our specimen is like *A. hypoleuca* with its purple, non-pointed anthers and pale green leaves which are smaller than those in *A. arguta* and broader than those of *A. melanandra*.

3. "*A. rufa*"

In hindsight, this is the least surprising of the name changes in the germplasm collection. *A. rufa* is so different from other *Leiocarpae* in many morphological features. According to A.R.F., successive Japanese botanists and Li (1952) have treated *A. rufa* as a variety of *A. arguta*. Liang does not discuss *A. rufa* as his work was limited to Chinese and Taiwanese *Actinidia*.

Our specimen originated from a Japanese experimental station on the eastern side of Kyushu in an area where *A. rufa* grows naturally.

The plant differs from *A. arguta* and other *Leiocarpae* in its firm, broad leaves borne on rusty tomentose shoots. The fruit are large (Nakai 1933), ellipsoidal and "spotted". A.R.F. suggests that the D.S.I.R. specimen

of *"A. rufa"* is more reminiscent of *A. callosa* in its: dark, rigid and thick leaves, and orange lenticellate bark. Like *A. callosa* the winter buds are dome-shaped, "winged" in profile, and covered in ginger tomentum. Both A.R.F. and I agree that the N.Z. plant cannot be allied with *Leiocarpae*. A.R.F. suggests that his plant may be a variety of *A. callosa*, but this hypothesis needs confirmation.

4. *"A. melliana"* (36/4/3a)

This plant is quite distinct from a representative plant of the 'real' *A. melliana* seen by A.R.F. at Guilin. The D.S.I.R. specimen seems similar to Liang's description of *A. fortunatii*, but (according to Liang) the latter plant has not been collected since 1906. The identity of this plant is uncertain, and is provisionally termed "hairy *hemsleyana*".

In summary, *Actinidia* identification is still controversial. However, for this thesis, the nomenclature currently used in N.Z. has been retained. The work from this thesis indicates that considerable further research on the taxonomy of *Actinidia* is warranted. Herbarium-voucher specimens of the D.S.I.R. plants are now being examined by Asian botanists for verification of their nomenclature.

References (Chapter 1 Addendum) : Not in general ref. list, pp. 230-241

Nakai, T. (1933)
Notulae ad Plantas Japoniae et Koreae XLIII.
Bot. Mag. (Tokyo) 47(556) : 235-267.

CHAPTER TWO

COMPARATIVE (VEGETATIVE) MORPHOLOGY OF "SUMMER-SHOOTS" IN SOME *Actinidia*

CHAPTER TWO

2.1 INTRODUCTION

Actinidia are morphologically diverse vines (= lianes) (Krüssmann 1984, Li 1952), which normally adopt a rambling or climbing form (Dunn 1911, Stapf 1926), but they may become bush-like on occasion (Dunn 1908, Kolbasina 1963, Vorobiev 1939). Within the highly managed environment of the orchard (Ferguson 1990c), a range of shoot types persists, each with a characteristic potential for growth and flowering. Horticulturists produce phenotype from genotype, in order to maximise the economic gains arising from fruit production.

The current taxonomic treatment of *Actinidia* presented in *Flora Reipublicae Popularis Sinicae* (Liang 1984), emphasises reproductive attributes of the vines such as: number, colour shape and degree of fusion of floral parts. The size, shape and colour of fruit and seeds are also recorded by Liang *loc.cit.* Diagnoses are based on vegetative characters such as solidity or lamellation of stem pith and the structural complexity and abundance of trichomes on the underside (abaxial surface) of the leaf (Dunn 1911, Li 1952; Liang 1984).

The "two-dimensional" qualities of vegetative characters have been emphasised in most taxonomic treatments of these vines, owing to a reliance on evidence obtained from herbarium specimens. However, earlier field-botanists such as Dunn (1911), Li (1952), Rehder (1951) and Sargent (1894a) were more aware of differences in the stature, vigour and overall form of the vines. They also perceived some of the morphological changes that arose from the growth and development of *Actinidia* shoots, which accounted for some anomalous identifications in herbarium material (Dunn 1911).

Applications of shoot form in taxonomy such as those of Sargent (1894b) and Halle, Oldemann and Tomlinson (1978), suggested that the taxonomic potential of vegetative characters in *Actinidia* might be explored from a more dynamic perspective, with a greater awareness of ptyxis (Davis and Heywood 1963) and its modification by growth (Hickey and Wolfe 1975) and mechanical factors (Givnish 1987).

Most drawings of *Actinidia* (e.g. Dunac 1899, Liang 1984) show that the leaf venation is intricate and morphologically complex, yet this is little explored in most descriptions of these plants. Li (1952) uses general vein morphology in his diagnoses, while Liang (1984) uses the conspicuous appearance of leaf venation in naming *A. venosa*. The taxonomic potential of leaf venation is therefore explored

in *Actinidia*, in the light of the recent revisions of venation terminology by Hickey (1973, 1979).

There have been several anatomical studies of leaves in *Actinidia* (Dunac 1899, Beauvisage 1920, Solereder 1908, Lechner 1915, and Metcalfe and Chalk 1950). The most recent of these (Gao 1988) pre-empted publication of some of the work in this chapter. Most authors have noted the occurrence of ergastic crystals, particularly raphides, which are characteristic of this genus. Lechner *loc. cit.* provided anatomical diagnoses for fourteen species of *Actinidia*, including nine of those described herein. Both Gao and Lechner noted the taxonomic value of variations in palisade, mesophyll structure and hair structure. Gao showed that the structure of the petiole near the leaf base was taxonomically constant in *Actinidia*. Despite these studies of leaf anatomy in *Actinidia*, our knowledge remains incomplete.Furthermore, none of the above works have addressed the anatomical features of commercial *Actinidia* cultivars.

This chapter is an attempt to evaluate the taxonomic potential of structural characters derived from summer shoots of *Actinidia*. Descriptions extend existing knowledge of shoot structure in *Actinidia*.

The aims of this chapter are as follows :

(1) To evaluate the genotypic components of shoot morphology as exhibited by 20-30 *Actinidia* vines in the D.S.I.R. germplasm collection, with appropriate reference to plants growing elsewhere in the wild or under cultivation.

(2) To explore experimentally, the taxonomic potential of *ca.* 60 vegetative characters, using multivariate analysis to generate possible taxonomic groups and to identify the taxonomic value of selected characters.

(3) To investigate aspects of the structure, development and possible mode of action of the "water-excreting" glands in leaves of *A. deliciosa* var. *deliciosa* cv. Hayward.

2.2 MATERIALS AND METHODS

This study is based upon plants obtained from the D.S.I.R. *Actinidia* germplasm collection.

2.2.1 Plant collection

Summer shoots were obtained from vines specified in (Table 2.1). Collections were made in May 1988 and in January 1989 following a month of continuous rainfall. Material obtained in January was described in a fully turgid

condition from vines in an active state of summer growth, with many juvenile shoots still present.

Shoot samples were harvested in plastic bags and refrigerated in a cold-room at 4°C, to allow for extended observation of plants in a living state. Herbarium specimens were prepared according to Lawrence (1951).

Field data obtained from these plants were verified the following season (Jan. 1990), by Dr A.R. Ferguson (Tables 2.2-2.5).

2.2.2 Descriptive terminology

Descriptive terms were derived from the following sources :

1.	general taxonomy	- Krüssmann (1984), Lawrence (1951) Radford *et al.* (1974); Stearn (1966)
2.	leaf venation	- Dilcher (1974), Hickey (1979); Spicer (1980).
3.	hydathodes	- Esau (1976), Fahn (1982); Wilkinson (1979).

2.2.3 Leaf form measurements

Exemplars, representative individuals, were selected for each of the "taxa", as in Zhang and Thorp (1986).

Samples were taken randomly from each of the exemplars ("taxa"), such that 20 leaves were obtained from the "outer" fully sunlit regions of the vine and a further 20 leaves were sampled from the "inner" shaded region of the vine. These regions were defined qualitatively and apply to the standard T-bar canopy system (Sale 1985).

Several leaf form measurements (Figure 2.1) were made with a ruler. Biomass calculations were measured directly or generated secondarily as ratio variables. Dry weights were determined after drying leaves in a vacuum oven for 4 days at 60°C.

2.2.4 Light microscopy of leaf surfaces

Initial observations of stem and leaf surfaces were made at magnifications of 10-50x using a stereoscopic microscope. These were corroborated with information derived from "leaf peels". Here leaves were painted with colourless nail varnish and replicas detached from leaves after air-drying, by peeling using the fingernails assisted by razor blades and forceps when necessary. Replicas were examined using Nomarski interference optics and photographed.

2.2.5 Scanning electron microscopy of leaf surfaces

Detailed observations of leaf surfaces were made using a Cambridge Stereoscan 250 Mk2 scanning electron microscope, operated at 8-20 kV, equipped with a Robinson backscatter detector.

Fresh leaves were affixed to aluminium stubs with copper conductive paint G.E.C. Electronics, Illinois, U.S.A.), as fresh leaves (see Robards 1978, after freeze-drying from liquid nitrogen (subcooled), or after critical-point-drying from CO_2, with prior dehydration in ethanol and amyl acetate series, as described by Fineran and Condon (1988). Specimens for S.E.M. were routinely coated with a 5-10 nm layer of gold-palladium using an Edwards model coater, or a Polaron E5000 sputter coater.

2.2.6 Internal organisation of leaves

Procedures for investigating the internal structure of leaves in *Actinidia* largely follow those of Condon and Fineran (1989).

2.2.6.1 *Light microscopy*

Leaves were trimmed into pieces 0.5-1 cm^2 x 1 mm thick and fixed at 20°C for 24 hrs under water vacuum in 2.5% glutaraldehyde, in a 0.075 M Na-Na phosphate buffer (pH 7.2) vehicle.

2.2.6.2 *Dehydration (Chemical)*

Tissue was dehydrated for 2 hr in an ethanol series for 20 min. in each of 10, 20, 40, 60; 80% grades with 2 x 30 min changes in absolute ethanol. Specimens were also re-evacuated at a lower surface tension, in 80 and 100% alcohol changes, in order to remove any oxygen adhering to hairs on the surfaces of leaves.

2.2.6.3 *Infiltration*

Material was infiltrated in mixtures of 25 and 75% JB4 water-miscible resin (Polysciences Inc.) dissolved in ethanol, for 2-3 weeks at each stage, initially at 4°C and subsequently at room temperature. Samples were agitated during infiltration as the resin was prone to an aerobic polymerisation as time increased.

2.2.6.4 *Polymerisation*

Polymerisation of resin was carried out at 20°C for 2-3 hrs in a belljar containing an atmosphere of nitrogen. Alternatively, oxygen was excluded during polymerisation by filling a flat-embedding cap to excess and overflowing the contents. A microscope slide was then lowered on top of the meniscus of resin

Table 2.1 Vines of *Actinidia* Lindl. examined.

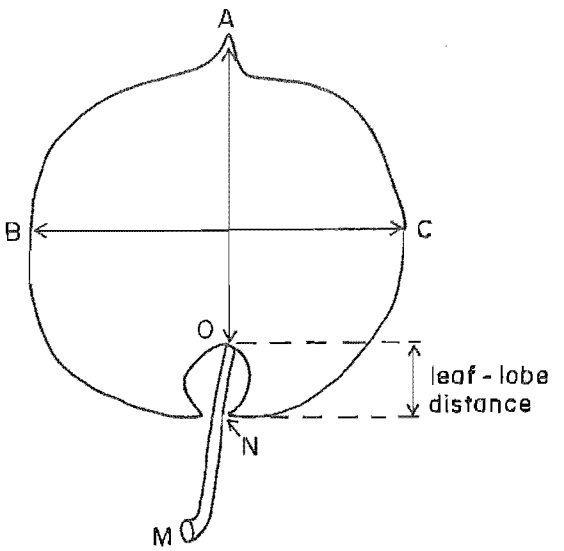
Taxa as recognised by Li (1952), Liang (1980, 1982a,b, 1983, 1984); Liang and Ferguson (1984, 1986).
Introduction and source categories : 1 = 1904, seeds, Japan; 2 = 1955, plants, England (original source not known); 3 = 1975, seeds, China; 4 = 1977, seeds, Japan; 5 = 1977, seeds, China; 6 = 1979, scionwood, USSR; 7 = 1981, seeds, China; 8 = 1981, scionwood, China; 9 = unknown, selection of Fletcher and Mouat.

Taxon	Orchard plant number(s)	Sex M/F	Intro and Source
Genus *Actinidia* Lindl.			
Section *Leiocarpae* (Dunn) Li			
Series *Lamellatae* C.F.Liang			
A. arguta (Sieb.et Zucc.) Planch. ex Miq.			
var. *arguta*	(T.P.)4/1/4	F	2
var. *cordifolia* (Miq.) Bean	(T.P.)4/1/16	F	2
A. rufa (Sieb. et Zucc.) Planch. ex Miq.	(T.P.)3/11/8 2nd vine	M	4
A. melanandra Franch.			
var. *melanandra*	(T.P.)4/1/9a	M	2
A. kolomikta (Maxim. et Rupr.) Maxim.	(T.P.)3/11/11	?[1]	6
Series *Solidae* C.F. Liang			
A. polygama (Sieb. et Zucc.) Maxim.	(T.P.)3/12/11	M	4
A. valvata Dunn	(K.)M1B1	M	7
Section *Maculatae* Dunn			
A. callosa Lindl.			
var. *henryi* Maxim	(T.P.)4/2/14b	M	2
A. chrysantha C.F. Liang	(T.P.)36/3/15a	M	7
A. indochinensis Merr.	(T.P.)36/3/8b	M	7
Section *Strigosae* Li			
A. melliana Hand.-Mazz	(T.P.)36/3/3a	M	7
A. hemsleyana Dunn			
var. *hemsleyana*	(T.P.)3/8/19a	M	3
Section *Stellatae* Li			
Series *Perfectae* C.F. Liang			
A. latifolia (Gardn. et Champ.) Merr.			
var. *latifolia*	(K.)M5B4	F	7
A. eriantha Benth.	(T.P.)3/7/15c	F	3
Section *Stellatae* Li			
Series *Perfectae* C.F. Liang			
A. chinensis Planch.			
var. *chinensis*	(T.P.)3/6/7a[2]	F	8
	(T.P.)3/6/9a[2]	F	8
	(T.P.)3/6/14b	F	5
A. deliciosa (A. Chev.) C.F. Liang et A.R. Ferguson			
var. *deliciosa*			
'Hayward'	(K.) destruction block	F	1
'Bruno'	(T.P.)4/5/16	F	1
'Matua'	(T.P.)4/2/16	M	9
var. *chlorocarpa* (C.F. Liang) C.F. Liang et A.R. Ferguson.	(K.)C6M2	F	7

Footnotes :
1. Sex unknown, plant not yet fruited.
2. These genotypes of *A. chinensis* var. *chinensis* have alternative names :
   3/6/7a = 460.4
   3/6/9a = 460.9
   Latter designations are used in results tables.

Abbreviations :
K = Kumeu Research Orchard, D.S.I.R., Fruit and Trees
T.P. = Te Puke Research Orchard, D.S.I.R., Fruit and Trees

Figure 2-1: Leaf Measurements



KEY

OA = leaf length
BC = leaf width
ON = leaf lobe distance
MO = petiole length

Based on n = 20 outer leaves per plant
and n = 20 inner leaves per plant

with an intervening piece of "Parafilm". Polymerisation was completed within 2-4 hrs at 20°C.

2.2.6.5 *Microtomy for L.M.*

Sections of leaves were obtained with a Reichert rotocut 2000 EX and with a Jung rotary microtome 11800 equipped with glass knives mounted in a modified knife-holder (Fineran and Johnston 1974).

2.2.6.6 *Staining for L.M.*

Sections were stained with one of the following histochemical reagents :

1. 50/50 methylene blue/toluidine Blue (aq)
2. acid fuschin (aq)/toluidine blue (aq) (Feder and O'Brien 1968).

After rinsing and drying slides on a hotplate for 2-3 min at 40-60°C, sections were mounted on slides in DPX-xylene based mountant and coverslips were added.

2.2.6.7 *Photomicrography for L.M.*

Bright-field micrographs were recorded on Ilford FP4 film using a Leitz Orthoplan photomicroscope equipped with an Orthomatt M400 camera. Films were developed in Rodinol F for 5-10 mins using a 1:20 dilution of developer to water.

2.2.7 Internal structure of leaves, S.E.M. methods

S.E.M. methods were also used to document for the chemical artifacts induced by most L.M. methods and also to document the three-dimensional form of the leaves.

2.2.7.1 *Preparation of fractured leaves for S.E.M.*

Leaves were prepared for S.E.M. following the freeze-fracture methods of Fineran and Condon (1988) and Condon and Fineran (1989). This involved material being immersed in subcooled liquid nitrogen ("slush"),[1] at -210 degrees C. (Robards and Sleytr 1988). The leaves were subsequently broken into pieces 1-2 cm^2 under the liquid and stored in small aluminium containers held in a large dewar of liquid nitrogen. For freeze-drying, the containers and their liquid nitrogen were transferred to a Bullivant-Ames device (see Fineran 1978) filled with liquid nitrogen) and placed in an Edwards vacuum coater unit for 11 hrs at a vacuum pressure of 2 x 10 Torr. The freeze-dried samples were then mounted on stubs, as described in Section 4.2.3.

2.2.7.2 *Photomicroscopy*

Scanning electron micrographs were recorded on Ilford FP4 developed in Microphen and rated at 200 ASA.

---

[1]"slush" is defined as "sub-cooled" liquid nitrogen maintained at its triple point (solid = liquid = gas; no distinction between phases) where the Nitrogen solidifies at 63K.

2.2.8 Internal structure of leaves T.E.M. methods

Schedule

2 hr fixation
2.5% Glutaraldehyde in 0.075M Na-Na phosphate buffer*
pH = 7.2 at 20°C

↓

post-fixation buffering*

↓

2-3 hr post-fixation
1% O_sO_4 in 0.025M Na-Na phosphate buffer
pH = 7.2 at 20°C

↓

post-fixation buffering*

↓

Chemical dehydration
10 min in 20,40,60;80% acetone (aq) with 3 x 10 min changes in 100% acetone

↓

Infiltration
30% Spurr's resin (Spurr 1969) in acetone overnight

↓

Embedment
100% Spurr's resin polymerised at 70°C

↓

Ultramicrotomy
blocks trimmed and sectioned with a diamond knife for T.E.M. on an LKB Ultrotome IV

↓

Post-staining of sections in uranyl acetate-lead citrate

↓

Transmission electron microscopy
JEOL 1200 EX Transmission electron microscope operated at 80-100 kV.

* Indicates same buffer used during fixation and post-fixation.

2.2.9 Cluster analysis of winter shoot characters

Cluster analysis (C.A.) is frequently used in taxonomic and morphometric studies to search for inherent groupings within large multivariate data sets. In C.A,

overall relationships between species or individuals are assessed in "distance" (variance-covariance) or "similarity" (correlation) matrices (Sneath and Sokal 1973). The three-dimensional clusters arising from C.A. are presented in two-dimensional computer-drawn diagrams termed phenograms.

Relationships between individuals (termed O.T.Us = operational taxonomic units) or exemplars of *Actinidia* taxa derived from winter shoot characters were assessed using Gower's (1971) general coefficient of similarity. Similarity values were clustered using complete, arithmetic group averages (U.P.G.M.A.) and single-linkage techniques. The degree of deviation of the phenogram from its precursor similarity matrix, was assessed using the cophenetic correlation coefficient of Sokal and Rohlf (1962).

The program used for C.A. was "Gower", written by Drs C.M. Frampton, G.A. Findlay and J.M. Ward, Christchurch.

2.2.9.1 *Characters*

Characters can be defined as attributes which taxonomists separate from whole organisms for particular purposes such as comparison or identification (Davis and Heywood 1963). Any character may be expressed (often arbitrarily) as a number of indivisible parts (henceforth termed "character states").

Variables or "characters" entered into the similarity matrix are coded as "multistate non-ordered", "discrete non-ordered" or "binary dichotomous" in category.

"Multistate ordered" or "type 1" characters in the computer program, also termed quantitative multistate characters, are those in which the character states can be placed in an ordered sequence. These characters may include a series of measurements along a scale, (e.g. leaf width in mm), or they may include other characters, which have been subdivided into a number of discrete character states, (e.g. leaf apex form as a character with 3 character states: 1 = acuminate, 2 = apiculate and 3 = retuse).

"Discrete non-ordered" or "type 2" characters in the program, are those in which character states cannot be placed in an ordered sequence and where both presence and absence character states are considered to be of equal importance in assessing similarity. "Type 2" characters include non-ordered multistate characters, for example petal colour with 3 character states: 1 = green, 2 = white, and 3 = yellow, and binary alternative characters such as leaf crystal form with character states : 1 = acicular and 2 = cubic.

"Binary dichotomous" or "type 3" characters are used when the sharing of one of the character states is regarded as a similarity, but the sharing of the second state is not, (e.g. two taxa would be regarded as similar if they had stellate hairs and dissimilar if they lacked them).

2.2.9.2 *Similarity coefficients*

Gower's general coefficient of similarity (1971) can be used with data containing different kinds of characters without the need for recoding. Gower's coefficient is a composite of three similarity coefficients. One of the three is chosen for each character in the data set. Jaccard's coefficient S_J is used with binary dichotomous characters (shared absence or negative state of the character not scored as a similarity), the simple matching coefficient S_{sm} is used with "discrete non-ordered" characters (sharing of any or either state of the character scored as a similarity). With "continuous" characters Gower applies the following coefficient

$$S_{ijk} = 1 - (|X_{ik} - X_{jk}|/R_k)$$

where X_{ik} is the score of OTU i for character k, X_{jk} is the score of OTU j for character k and R_k is the range of character k.

The simple matching coefficient of Sokal and Michener (1958) is defined as :

$$S_{SM} = (Nsp + Nsn)/(Nsp + Nsn + Nu)$$

and Jaccard's coefficient (1908) is defined as :

$$S_J = Nsp/(Nsp + Nu)$$

where Nsp is the number of states whose presence or positive state is shared by two OTUs, Nsn is the number of shared absence or negative states in the two OTUs being compared with Nu is the number of unshared states (i.e. present/positive in one and absent/negative in the other of the two OTUs being compared). The simple matching coefficient gives equal weight to the shared presence/positive state and absence/negative state of characters, while Jaccard's coefficient ignores shared absences/negative states.

2.2.9.3 *Cluster methods*

The similarity values were clustered by the unweighted pair group method using arithmetic averages (UPGMA) and by the single linkage technique.

In UPGMA, and OTU has a similarity to an existing cluster equal to its average similarity to the members of the cluster (Sokal and Michener 1958). The similarity between two clusters is equal to the average similarity of all members of

one cluster with all members of the other. Average-linkage provides information on average phenetic relationships. The clusters form over an intermediate range (compared with single and complete linkage clustering) and the hierarchical structure is quite clear. Average-linkage generally gives the least amount of distortion of a similarity matrix (Rohlf 1970, Sneath and Sokal 1973). However, outlying OTUs (those which are not similar to any others) may form a pair not because they are most similar to each other, but rather because their similarity to each other is higher than either one's average similarity to any existing cluster.

In single linkage clustering, an OTU has a similarity to an existing cluster which is equal to its similarity to the closest member within the cluster. The single linkage technique (Florek *et al.*, 1951 a,b and Sneath 1957) provides information on closest phenetic relationships, and because of the criterion for entry into the fusion of clusters, it is not sensitive to cluster size.

2.2.9.4 *Cophenetic correlation coefficient*

Since the phenogram resulting from C.A. is a two-dimensional representation of a multi-dimensional structure, some distortion of the relationships in the similarity matrix on which it is based is inevitable. The "degree of fit" of a phenogram to the similarity matrix from which it is derived may be measured using the cophenetic correlation coefficient proposed by Sokal and Rohlf (1962). [A matrix of cophenetic values is obtained from the phenogram by finding the similarity level that links each pair of OTUs. The cross-product correlation coefficient is then computed between the two matrices; this is the cophenetic correlation coefficient]. A value of one represents complete agreement between the two matrices.

Sections 2.2.9.2 to 2.2.9.4 were adapted, with permission, from Breitwieser (1990) with minimal modifications. Methods used in these sections of the thesis are identical to those used by Breitwieser *loc. cit.*

2.2.10 **Discriminant analysis (D.A.) of summer shoot characters**

The character set (Appendix 2.2.1) used in this chapter is large and diverse and most (binary and continuous multistate) are not suited to discriminant analysis. D.A. is explained and demonstrated more comprehensively in Chapter Three (Section 3.3.3). Throughout this thesis D.A. is synonymous with the "standard type of discriminant analysis" (Frampton 1988) as devised by Fisher (1936). It is not to be confused with "stepwise discriminant analysis", which is a refined discriminant procedure outside the scope of this exploratory investigation. D.A. was performed using the SYSTAT statistical package.

2.3 RESULTS

2.3.1 Comparative morphology of summer shoots in some *Actinidia* under cultivation

Actinidia vines in the spring and summer months are colourful and handsome plants of extremely varied morphology. The vegetative form of these plants is described in detail in Tables 2.2 - 2.6, but the main trends are summarised in the following text.

2.3.1.1 *Stem characters*

The colour of 2 yr canes (Table 2.2) is generally more stable than that of the current year's wood. None of the colours appear to be unique to particular sections of the genus. Two year old wood is generally brown or brown overlain with blue-green pigmentation. Red-purple colours are more common in the *Stellatae* but are not restricted to this group.

Cane texture results from a combination of the underlying bark and any overlying hairs or lenticels. The wood is coarsely textured in sections *Leiocarpae*, *Maculatae* and *Strigosae*. The underlying bark may be lustrous with large warty lenticels, e.g. *A.* polygama. Preliminary anatomical observations show that lenticel protuberance is proportional to the depth of the concave depression formed by the phellogen. The bulk of the lenticel is filled with parenchymatous "packing tissue".

Canes of the *Stellatae* are more finely textured, with a rough (asperous) texture arising from a cover of stiff (hispid) hairs, which may persist as intact structures in the form of "stubble" or hair bases only (see Chapter Three for details).

The colour and form of lenticels (Table 2.2) can be used to identify spring and summer shoots. Most *Actinidia* have orange or brown, but rarely, yellow or white lenticels. *Stellatae* have smaller lenticels with white edges and orange to brown centres.

The length of internodes (Table 2.2) of the current year's canes is characteristic of certain sections of the genus. *Leiocarpae* have the shortest canes, those of the *Maculatae* and *Strigosae* are comparable in length or longer, whereas, *Stellatae* have the longest internodes in the genus.

Table 2.2(a) Stem Characters in some *Actinidia* Taxa

Taxon	2 yr cane colour	2 yr cane texture
A. arguta var. *arguta*	brown to blue-green	smooth, polished
A. arguta var. *cordifolia*	light greyish brown white lenticels	smooth, polished raised lenticels
A. rufa	grey to brown	rough
A. melanandra var. *melanandra*	light green to blue green	lumpy, warty
A. kolomikta	chestnut brown	warty, rough
A. polygama	chestnut brown	rough, ruptured
A. valvata	purple-black	very rough, fissured
A. callosa var. *henryi*	pale brown	warty, rough
A. chrysantha	purple to brown	warty
A. indochinensis	chestnut brown	smooth
A. melliana	blue-green to brown at base	bristly
A. hemsleyana var. *hemsleyana*	red-purple to white-brown underside	warty, rough
A. latifolia	dark purple-brown to blue-green underside	glossy
A. eriantha	blue-green to brown or purple. Hairs give a blue-white hue	soft downy, felty
A. chinensis var. *chinensis* 3/6/14b*	chocolate brown with a silver grey hue	rough, asperous
A. chinensis var. *chinensis* 460.4*	same	rough, asperous
A. chinensis var. *chinensis* 460.9*	same	rough, asperous
A. deliciosa var. *deliciosa* 'Hayward'	light brown to ash-grey	rough, asperous
A. deliciosa var. *deliciosa* 'Matua'	green brown to blue-grey	rough, asperous
A. deliciosa var. *deliciosa* 'Bruno'	red-purple to brown blue-green in shade	rough, asperous
A. deliciosa var. *chlorocarpa*	very subtle red-purple to brown	rough, ridged, asperous

Continued .....

Footnotes : * numbers are different genotypes.

Taxon	1 yr cane colour	1 yr lenticels profile colour shape
A. arguta var. *arguta*	greyish-green more exposed canes reddish brown above	low cream some elongate, some spherical
A. arguta var. *cordifolia*	purplish/brown to brown-red	prominent orange-brown elongate
A. rufa	green to brown	prominent orange-brown elongate
A. melanandra var. *melanandra*	brown to red with blue-green hue	prominent orange-yellow elongate
A. kolomikta	chestnut brown green underside	prominent yellow-brown more spherical
A. polygama	green to brown	prominent orange-brown most elongate, some spherical
A. valvata	green to brown	prominent orange-brown elongate
A. callosa var. *henryi*	green to brown	prominent yellow-white elongate
A. chrysantha	green to brown	prominent orange-white extremely elongate
A. indochinensis	mid brown to chestnut brown	low orange-white extremely elongate
A. melliana	blue-green to light green	low white-cream-orange extremely elongate
A. hemsleyana var. *hemsleyana*	blue-green to brown younger canes green	prominent orange-brown spherical to elongate
A. latifolia	green to purple-brown younger green to pink	low white-orange-brown elongate
A. eriantha	blue-green to grey white	low white-orange-brown elongate
A. chinensis var. *chinensis* 3/6/14b*	green-brown with blue-green hue	prominent white-cream-orange elongate & spherical
A. chinensis var. *chinensis* 460.4*	same	same
A. chinensis var. *chinensis* 460.9*	same	same
A. deliciosa var. *deliciosa* 'Hayward'	chocolate-brown with red-hue, underside blue-geeen	prominent white-cream spheroid
A. deliciosa var. *deliciosa* 'Matua'	geeen-white with pink to red over-tones	prominent orange elongate & spherical
A. deliciosa var. *deliciosa* 'Bruno'	red, purple-brown blue-green under-side	prominent orange-white cream surround elongate & spherical
A. deliciosa var. *chlorocarpa*	green to brown hairs give red hue	prominent white elongate.

Continued .....

Footnote : * Numbers are different genotypes

Table 2.2(c) Stem Characters in some *Actinidia* Taxa

Taxon	1 yr cane (mm) internode length	
A. arguta var. *arguta*	short medium	30-40 50-60
A. arguta var. *cordifolia*	short medium	20-40 60-70
A. rufa	short medium	30-40 60-80
A. melanandra var. *melanandra*	short medium	30-40 50-60
A. kolomikta	medium	60-70
A. polygama	medium long	50-70 90-150
A. valvata	short medium	30-40 60-90
A. callosa var. *henryi*	short medium	30-40 50-60
A. chrysantha	short medium	30-40 70-90
A. indochinensis	short short to medium	30-40 40-60
A. melliana	very short medium to long	20-40 60-100
A. hemsleyana var. *hemsleyana*	short to medium medium	50-60 60-80
A. latifolia	short medium	30-40 60-70
A. eriantha	short to medium medium	50-70 60-70
A. chinensis var. *chinensis* 3/6/14b*	medium very long	40-60 100-150
A. chinensis var. *chinensis* 460.4*	same	
A. chinensis var. *chinensis* 460.9*	same	
A. deliciosa var. *deliciosa* 'Hayward'	medium very long	60-70 100-150
A. deliciosa var. *deliciosa* 'Matua'	long to medium very long	70-80 100-150
A. deliciosa var. *deliciosa* 'Bruno'	medium to long very long	60-80 120-170
A. deliciosa var. *chlorocarpa*	short to medium very long	30-40 100-150

Footnote : * Numbers are different genotypes

2.3.1.2 *Leaf characters*

Petioles show few distinctive trends in colour and surface morphology across the genus. Shaded petioles are green or golden, becoming fuchsia-pink to red in sunlit shoots. Petioles may be grooved along their uppermost surfaces and this has an anatomical basis (Section 2.3.4).

Petioles of *Stellatae* are longer than those of most *Actinidia* (Table 2.3), with these being twice the length of most *Leiocarpae* studied and were up to three times longer than those of the *Maculatae* and *Strigosae.*

The three-dimensional form of the leaf and its components (Table 2.3) varies markedly among different sections of the genus. The leaf position in relation to the plane of the cane (p.o.c.) is supra-horizontal or hanging, without any obvious trends among taxonomic groups.

The course and emergence of the petiole is difficult to describe without detailed studies of shoot phyllotaxy. I have deliberately avoided phyllotaxis, since this is known to change with the development of the *A. arguta* shoot, during the growing season (Pulawska 1965). It is also difficult to determine phyllotaxis from pruned shoots.

Leaves of most *Actinidia* arise from buds at 90° angles to the axis and petioles subsequently orient themselves, so that the leaf blades intercept light in a common plane, along the right or left-hand side of the cane. Buds may be disposed at any point within a 360° angle about the cane. Petioles may commonly have "J-shaped" bases to bring leaves of lower or sidewards pointing buds into the common plane. Buds of vines such as *A. chrysantha* (Plate 2.1D) and *A. indochinensis* have sideways and upwardly pointing buds which break from canes at 90° angles and then curve acutely upward for light interception. *A. deliciosa* has many downwardly pointing buds and a more complex phyllotaxy with lots of J-shaped petiole bases.

The three-dimensional form of the blade as a whole may be taxonomically informative. Leaf blades or laminas of most *Leiocarpae* are strongly arched from the base to the apex of the leaf (Plate 2.1E). Most *Stellatae* have mature leaves which are almost planar for $\geqslant \frac{3}{4}$ of their length (Plate 2.1C), with a profile descending only gently toward the base and apex of the blade. *A. latifolia* is the exception to this trend in having leaves folded in halves along the length of the midrib. There is a tendency for leaves of most *Actinidia* to become increasingly planar with maturity, although this is a gradual trend in comparison to the differences described. Leaves of many *Actinidia* rise upward in a convex manner in between the veins, (e.g. *A. deliciosa*) and can thus be described as bullate.

Habit shots of selected *Actinidia* taxa.

PLATE 2.1:

A Obviously bullate leaves of *A. rufa*.

B Shoot dimorphism in *A. deliciosa* var. *deliciosa* cv. Hayward. "Long-shoots" with apiculate, widely ovate leaves and basal "short-shoots" with orbicular leaves and retuse apices.

C Three-dimensional form of leaves in *A. deliciosa* var. *deliciosa* cv. Hayward. Leaves suprahorizontal (above plane of cane), bullate; overlapping basal lobes evident. Stems chocolate brown and petioles pink. Buds emerge at all points but leaves align in a common plane.

D Leaves of *A. chrysantha* arising from upward and sideways pointing buds along a one year old stem.

E Bullate, yellow-green; membraneous leaves of *A. valvata* arising from dark coloured shoots with warty lenticels.

F Close-up view of leaf in *A. deliciosa* var. *deliciosa* cv. Hayward. Overlapping cordate basal lobes, bullate tissue between lateral (secondary) veins and strongly percurrent (adjoining laterals at 90°) tertiary veins are evident in these leaves.

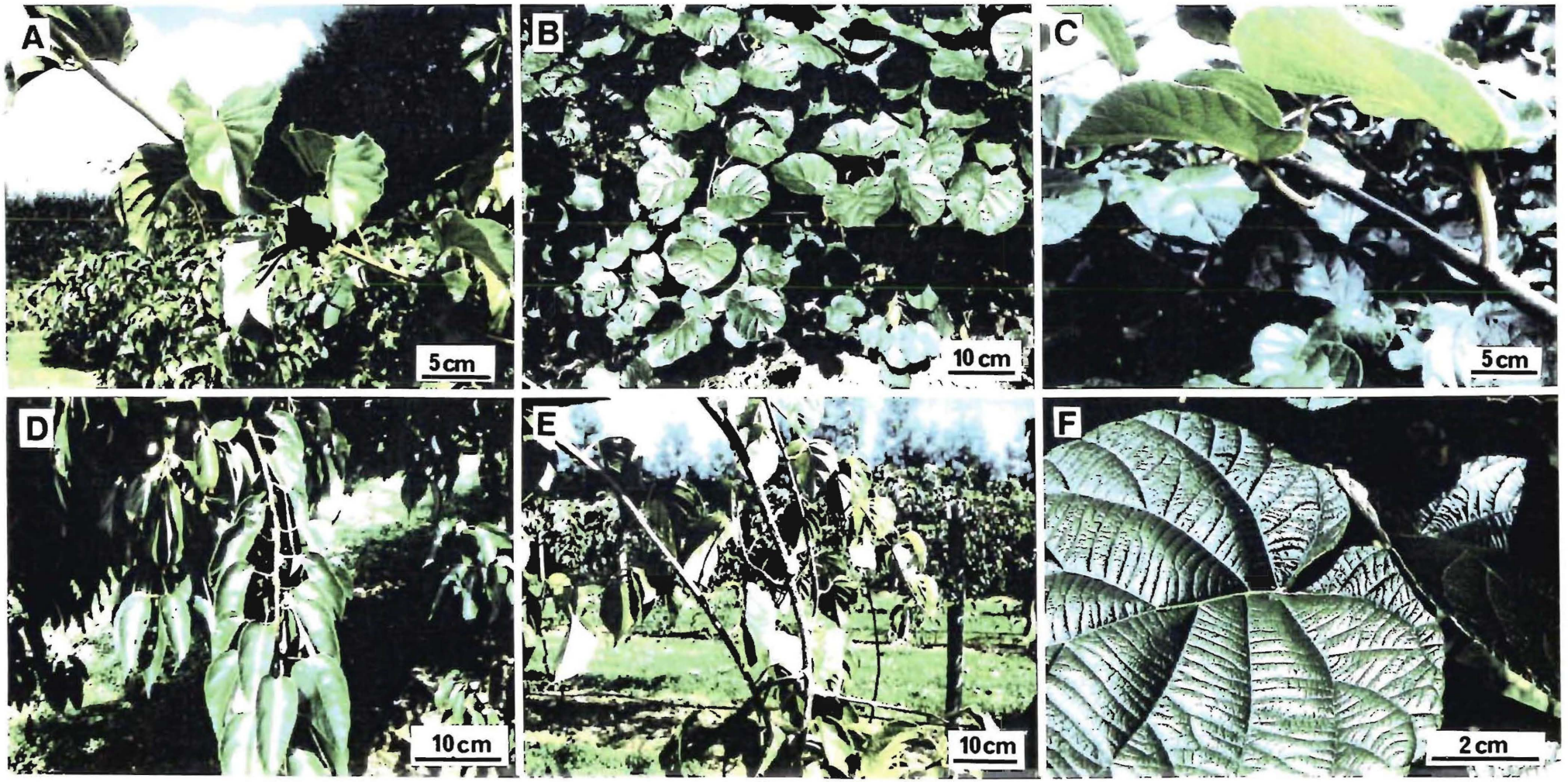

A
5 cm
B
10 cm
C
5 cm
D
10 cm
E
10 cm
F
2 cm

Table 2.3(a) Leaf Characters in some *Actinidia* Taxa

Taxon	petiole colour surface	petiole length : lamina
A. arguta var. *arguta*	pink to rusty red (sun) green in shade glabrous	1:1 sun 1:3 shade
A. arguta var. *cordifolia*	paler in shade grooved above brownish purplish pink, green just at base developed white spines on old petioles	short 1:3–4
A. rufa	green with red-brown hue due to hairs	short 1:3–4
A. melanandra var. *melanandra*	yellow-green, pink at base, young petioles bright red dorsal ridging	very short 1:4–5
A. kolomikta	yellow to white dorsal ridging glabrous	short 1:5
A. polygama	strong pink to red at base green elsewhere petiole 3-ribbed	short to long 1:2–3
A. valvata	red in sun, yellow-green near base, pink elsewhere grooved above	short to long 1:2–3
A. callosa var. *henryi*	yellowish green groved above brown hair bases yellow petioles pinkish	short 1:3–4
A. chrysantha	pink to red upper side pink to green lower basal brown hairs; grooved	short 1:3–5
A. indochinensis	yellow-green same as leaves	very short 1:4–5
A. melliana	blue-green below pink above	very short 1:10
A. hemsleyana var. *hemsleyana*	pale-yellow green covered in dense ginger hairs, especially younger leaves reducing to hair bases deeply grooved	very short 1:4–5
A. latifolia	yellow-green, blue-green near bases, red purple at bases of water shoots	short to long 1:2–3
A. erianthа	blue-green to white tomentose	short 1:6
A. chinensis var. *chinensis* 3/6/14b*	pink to red in sun light green beneath orange-brown hairs	long 1:2
A. chinensis var. *chinensis* 460.4*	same	same
A. chinensis var. *chinensis* 460.9*	same	same
A. deliciosa var. *deliciosa* 'Hayward'	pink to red entire length soft red-brown hairs	short 1:1–2
A. deliciosa var. *deliciosa* 'Matua'	yellow-green with pink hue, hairs? grooved above	long 1:1–2
A. deliciosa var. *deliciosa* 'Bruno'	light pink to red with orange-brown hairs	very long 1:1
A. deliciosa var. *chlorocarpa*	red-purple above yellow-green to blue-green near base	long 1:1–2

Continued .....

Footnote : *Numbers are different genotypes

Table 2.3(b) Leaf Characters in some *Actinidia* Taxa

Taxon	leaf position re. plane of cane (p.o.c.)	petiole emergence and course
A. arguta var. *arguta*	horizontal to slightly arched apex below p.o.c.	arise from node at 45° J shaped base
A. arguta var. *cordifolia*	suprahorizontal arching	arise from node at 45° J shaped base
A. rufa	suprahorizontal cascading apex below p.o.c.	arise from node at 90° curve upward 50-60° above poc
A. melanandra var. *melanandra*	vertical to limp hanging apex below p.o.c.	arise from node at 90° usually curved upwards so proximal part of leaf above
A. kolomikta	suprahorizontal descending apex below p.o.c .	arise from node at petioles don't flick and turn to reorient lamina
A. polygama	base suprahorizontal lamina mostly descending apex below p.o.c.	arise from node at 90° curve upwards at 45° to bring lamina horizontal
A. valvata	hanging below p.o.c.	arise from node at 90° curve upwards at 45° to bring lamina horizontal
A. callosa var. *henryi*	suprahorizontal gently arching above p.o.c.	arise from node at 90° curve upwards at 45° to bring lamina horizontal
A. chrysantha	hanging below base above p.o.c. but hanging down almost limply	arise from node at 90° don't flick and turn to reorient leaf
A. indochinensis	arched downwards hanging apex below p.o.c.	arise from node at 90° don't flick and and turn to reorient leaf.

Continued ....

Table 2.3(b)Cont... Leaf Characters in some *Actinidia* Taxa

Taxon	leaf position re. plane of cane (p.o.c.)	petiole emergence and course
A. melliana	outer leaves hang and apices point to base of cane.	arise from node at 45° - 90° subject to bud orientation
A. hemsleyana var. *hemsleyana*	centre and top of vine leaves point older leaves arched above p.o.c., elsewhere descending	petiole bases J-shaped mostly curve upwards at 45°
A. latifolia	base suprahorizontal lamina mostly descends below p.o.c.	side and lower pointing buds common, petiole bases J-shaped
A. eriantha	older leaves horizontal to descending below p.o.c.	arise from node at 90° curve upwards at 45° J-shaped petiole bases
A. chinensis var. *chinensis* 3/6/14b*	suprahorizontal slight arching near base	arise from node at 90° curve upwards at 45° J-shaped petiole bases
A. chinensis var. *chinensis* 460.4*	same	same
A. chinensis var. *chinensis* 460.9*	same	same
A. deliciosa var. *deliciosa* 'Hayward'	suprahorizontal slight arching near base	many side and lower pointing buds. Petioles curve upwards at 50°-60° J-shaped petiole bases
A. deliciosa var. *deliciosa* 'Matua'	suprahorizontal leaves whorled	arise from node at 45° little twisting no J-shaped bases, leaf is whorled
A. deliciosa var. *deliciosa* 'Bruno'	horizontal approaching p.o.c.	arise from bud at 90° curve upwards at 60-80° angle sharply
A. deliciosa var. *chlorocarpa*	horizontal approaching p.o.c.	lots of J-shaped bases due to lower and side pointing buds

Footnote : *Numbers are different genotypes

Table 2.4(a)
Leaf Shape Characters in Mature Leaves of some *Actinidia* Taxa
(also recorded in the wild by Liang 1984)

Taxon	mature leaf shape	leaf thickness
A. arguta var. *arguta*	widely ovate[1] orbicular	chartaceous to to coriaceous
A. arguta var. *cordifolia*	ovate to widely ovate	coriaceous
A. rufa	ovate	coriaceous ovate
A. melanandra var. *melanandra*	variable: ovate or lanceolate	coriaceous
A. kolomikta	ovate	chartaceous to coriaceous
A. polygama	ovate to widely ovate	membranaceous
A. valvata	ovate	membranaceous
A. callosa var. *henryi*	widely ovate	coriaceous to chartaceous
A. chrysantha	ovate	coriaceous
A. indochinensis	ovate	coriaceous
A. melliana	lanceolate	coriaceous
A. hemsleyana var. *hemsleyana*	wide elliptic to ovate	coriaceous
A. latifolia	widely ovate	coriaceous
A. eriantha	ovate to widely ovate	coriaceous
A. chinensis var. *chinensis* 3/6/14b*	widely ovate orbicular	coriaceous
A. chinensis var. *chinensis* 460.4*	widely ovate orbicular	coriaceous
A. chinensis var. *chinensis* 460.9*	widely ovate orbicular	coriaceous
A. deliciosa var. *deliciosa* 'Hayward'	widely ovate orbicular	coriaceous
A. deliciosa var. *deliciosa* 'Matua'	widely ovate orbicular	coriaceous
A. deliciosa var. *deliciosa* 'Bruno'	widely ovate orbicular	coriaceous
A. deliciosa var. *chlorocarpa*	widely ovate orbicular	chartaceous

Continued .....

Footnote : * Numbers are different genotypes

Leaf Shape Characters in Mature Leaves of some *Actinidia* Taxa
(also recorded in the wild by Liang 1984)

Taxon	leaf apex	variability of bases[2] symmetry of bases
A. arguta var. *arguta*	apiculate orbicular	variable asymmetric
A. arguta var. *cordifolia*	apiculate	variable occ. asymmetric
A. rufa	acuminate curled, twisted	variable occ. asymmetric
A. melanandra var. *melanandra*	acuminate curled, twisted	more consistent asymmetric
A. kolomikta	acuminate curled, twisted	variable symmetric
A. polygama	acuminate to long apiculate curled, twisted	variable symmetric
A. valvata	acuminate to long apiculate	variable occ. asymmetric
A. callosa var. *henryi*	acuminate to long apiculate	variable occ. asymmetric
A. chrysantha	acuminate to long apiculate	rather variable asymmetric
A. indochinensis	acuminate	more consistent occ. asymmetric
A. melliana	very long apiculate	variable symmetric
A. hemsleyana var. *hemsleyana*	acuminate to long apiculate	more consistent asymmetric
A. latifolia	acuminate apex hooked, twisted	variable us. symmetric
A. eriantha	acuminate	rather variable occ. asymmetric
A. chinensis var. *chinensis* 3/6/14b*	long shoots - apiculate short shoots- retuse - emarginate	consistent[2] symmetric
A. chinensis var. *chinensis* 460.4*	long shoots - apiculate short shoots - retuse - emarginate	consistent[2]
A. chinensis var. *chinensis* 460.9*	long shoots - apiculate short shoots - retuse - emarginate	consistent[2]
A. deliciosa var. *deliciosa* 'Hayward'	long shoots - apiculate short shoots - retuse	consistent[2] symmetric
A. deliciosa var. *deliciosa* 'Matua'	long shoots - apiculate short shoots - retuse	consistent[2] symmetric
A. deliciosa var. *deliciosa* 'Bruno'	long shoots - apiculate short shoots - retuse	variable symmetric
A. deliciosa var. *chlorocarpa*	long shoots - apiculate short shoots - retuse	consistent[2] slight asymmetry

Continued .....

Footnote: : * Numbers are different genotypes

Leaf Shape Characters in Mature Leaves of some *Actinidia* Taxa
(also recorded in the wild by Liang 1984)

Taxon	leaf base types (Radford *et al.* 1974)
A. arguta var. *arguta*	cuneate oblique truncate dim. cordate
A. arguta var. *cordifolia*	cordate truncate
A. rufa	oblique dim. cordate dim. truncate
A. melanandra var. *melanandra*	cuneate obtuse occ. truncate
A. kolomikta	rounded dim. cordate
A. polygama	rounded truncate cordate
A. valvata	obtuse oblique truncate
A. callosa var. *henryi*	oblique cordate bases slightly overlapping
A. chrysantha	oblique truncate rounded dim. cordate dim. obtuse
A. indochinensis	cuneate oblique
A. melliana	rounded cuneate dim. cordate
A. hemsleyana var. *hemsleyana*	rounded occ. cuneate (young) rarely dim. cordate
A. latifolia	truncate rounded oblique dim. cordate
A. eriantha	oblique truncate rounded cuneate dim. cordate
A. chinensis var. *chinensis* 3/6/14b*	cordate inner lvs variable
A. chinensis var. *chinensis* 460.4*	same as 3/6/14b
A. chinensis var. *chinensis* 460.9*	same as 3/6/14b
A. deliciosa var. *deliciosa* 'Hayward'	cordate bases markedly overlapping
A. deliciosa var. *deliciosa* 'Matua'	cordate bases markedly overlapping
A. deliciosa var. *deliciosa* 'Bruno'	obtuse cordate bases overlapping or not so
A. deliciosa var. *chlorocarpa*	cordate shallow open sinuses (bases)

Footnotes :

[1] Widely ovate is synonymous with broadly ovate.

[2] Variability of leaf bases in *A. deliciosa* and *A. chinensis* is markedly greater in the inner lvs borne on short shoots; outer lvs are us. consistent

* Numbers are different genotypes

Abbreviations :

dim = diminuitively; occ = occasionally; lvs = leaves; us = usually

Leaf shape characters (Table 2.4) are frequently used by taxonomists (e.g. Liang 1984) in descriptions of plants. Application of the internationally standardised terminology for leaf shape (S.Y.S.T.A.N.Z. 1962), reveals that most *Actinidia* have ovate or widely ovate leaves, but *A. chinensis*, *A. deliciosa* and *A. arguta* var. *arguta* have orbicular (circular) leaves, particularly on the "short" inner-most shoots arising near the centre of the vine.

The form of the leaf apex is apiculate to acuminate in the *Leiocarpae*. Leaf apices are curled and twisted in the *Lamellatae*, whereas, those of series *Solidae* are arched in the one plane only. *Maculatae* and *Strigosae* have apiculate or acuminate leaf tips. *A. chinensis* and *A. deliciosa* are very dimorphic vines bearing "long" and "short" (Wetmore and Garrison 1959) shoots, the extremes of which are typified by "apiculate" or "retuse" apices. Some shoots have irregularly notched or "emarginate" apices (Plate 2.1B).

Leaf bases are diverse and are diagnostic in most *Actinidia* observed. There is a marked tendency for cordate leaf apices in *A. chinensis* and *A. deliciosa*; the morphology of the basal lobes whether touching or overlapping is a useful guide to cultivar identification in *A. deliciosa* (Plates 2.1C; F).

2.3.1.3 *Juvenile shoots (Table 2.5, Plate 2.2)*

Previous authors (Brundell 1975a, Dunn 1911, Li 1952) have noted the morphological diversity exhibited by shoots of *Actinidia*. One year old shoots of 1-3 m in length and arising from 2 yr canes, are basically juvenile in character, within the first 0.5 m from the apex. Juvenility in this account is manifest by a continuous gradation of leaf shape from variously lanceolate or trullate leaves through to the ovate leaves, which typify mature shoots of most *Actinidia*. The *Leiocarpae* (Plates 2.2B;D) and *Strigosae* have lanceolate rather than ovate leaves at maturity in plants examined in this study. The range of leaf shape is most marked in the vines of the *Stellatae* examined in this survey. Maturity is defined as the point at which leaf shape and shoot pigmentation cease to change.

Juvenility can also entail changes in the course and gross morphology of the shoot as a whole, where "rat-tail" shoots are particularly evident in some taxa such as *A. arguta*. Many of the *Stellatae* have distally spiralling shoots which undergo pronounced helical growth in clockwise or anticlockwise directions, particularly upon contact with other objects. Such spiral growths may surround other branches or objects, as part of the adaptive "anchoring response" associated with the upward course of the lianoid growth habit. This growth form differs from the more randomly directed growth surges which can arise shortly after pruning.

The most conspicuous signs of juvenility involve striking colour changes

associated with young stems *per se*. In some *Maculatae* or *Strigosae* juvenile shoots are basically green in colour, albeit brighter than the adult shoots (Plate 2.2A). Most *Leiocarpae* and *Stellatae* have green or bright green foliage with relatively large quantities of red-brown or purple pigments, which may even mask the colour of the chlorophyll. Within a distance of 1-2 m from the apex this "accessory pigmentation" becomes confined to interveinal and marginal regions of the leaf. Subtle variations in the accessory pigments of shoots can be used to distinguish some cultivars of *A. deliciosa* (e.g. the greater intensity of purple-brown colouring in cv. Bruno.)

Much, if not all, the colour of juvenile shoots (Table 2.5) can be due to the indument clothing the surfaces. The density and pigmentation of the indument may caste a completely red, purple (e.g. *A. callosa* var. *henryi*, Plate 2.2E), or white hue (e.g. *A. eriantha*, Plate 2.2C) to the distal regions of the shoot. The scarlet to crimson red pigments in the hairs of *A. deliciosa 'Hayward' and A. melliana* shoots may darken to a brown colouring with age or exposure to the sun.

Within a short distance from the apex, the hairs soon abscise, but even the presence of their bases can impart a red or brownish hue to the surface of the shoot, e.g. *A. indochinensis* (Plate 2.2A). Hair bases can persist almost indefinitely in some taxa, at times imparting a pile-like or "villous" texture to the surfaces of the abaxial veins, e.g. *A. deliciosa.*

The colour and persistence of hairs can be related to the type of hair or "trichome". Most juvenile shoots are clothed with simple (unbranched), single-rowed (uniseriate) hairs, which are often red-brown or purple in colour. In most *Actinidia* these hairs abscise, leaving only vestiges in the form of pigmented hair bases. Young shoots of *A. melliana* and *A. eriantha* are unusual because the indument persists almost indefinitely as entire hairs on 1-2 yr old shoots.

Juvenile leaves of the *Stellatae* have uniseriate red-brown hairs, as well as white stellate (star-shaped) hairs. Only the stellate hairs persist in an intact form on the underside of the leaf, whereas, simple hairs abscise; except in the axils of lateral veins, near the petiole base or near the bases of the major (primary and secondary) veins along the uppermost (adaxial) surface.

Distal (apical) shoots of *Actinidia* with juvenile characters

PLATE 2.2:

A Lanceolate to ovate leaves; caducous ginger indument in *A. indochinensis* (*Maculatae*).

B Linear to lanceolate leaves of *A. arguta* var. *arguta* (*Leiocarpae*); pulverent hairs near bases of leaf blades.

C Widely ovate leaves and incanescent juvenile shoots of *A. eriantha* (*Stellatae*).

D Ovate leaves of red-purple pigmentation; finely tomentose stems of *A. kolomikta* (*Leiocarpae*).

E Ovate to widely ovate leaves of *A. deliciosa* var. *deliciosa* cv. Bruno (*Stellatae*). Red-brown hairs near apex, on major veins of abaxial surface and toward base of primary vein (midrib) on adaxial (uppermost) surface of leaf.

Bar scale = 10 mm

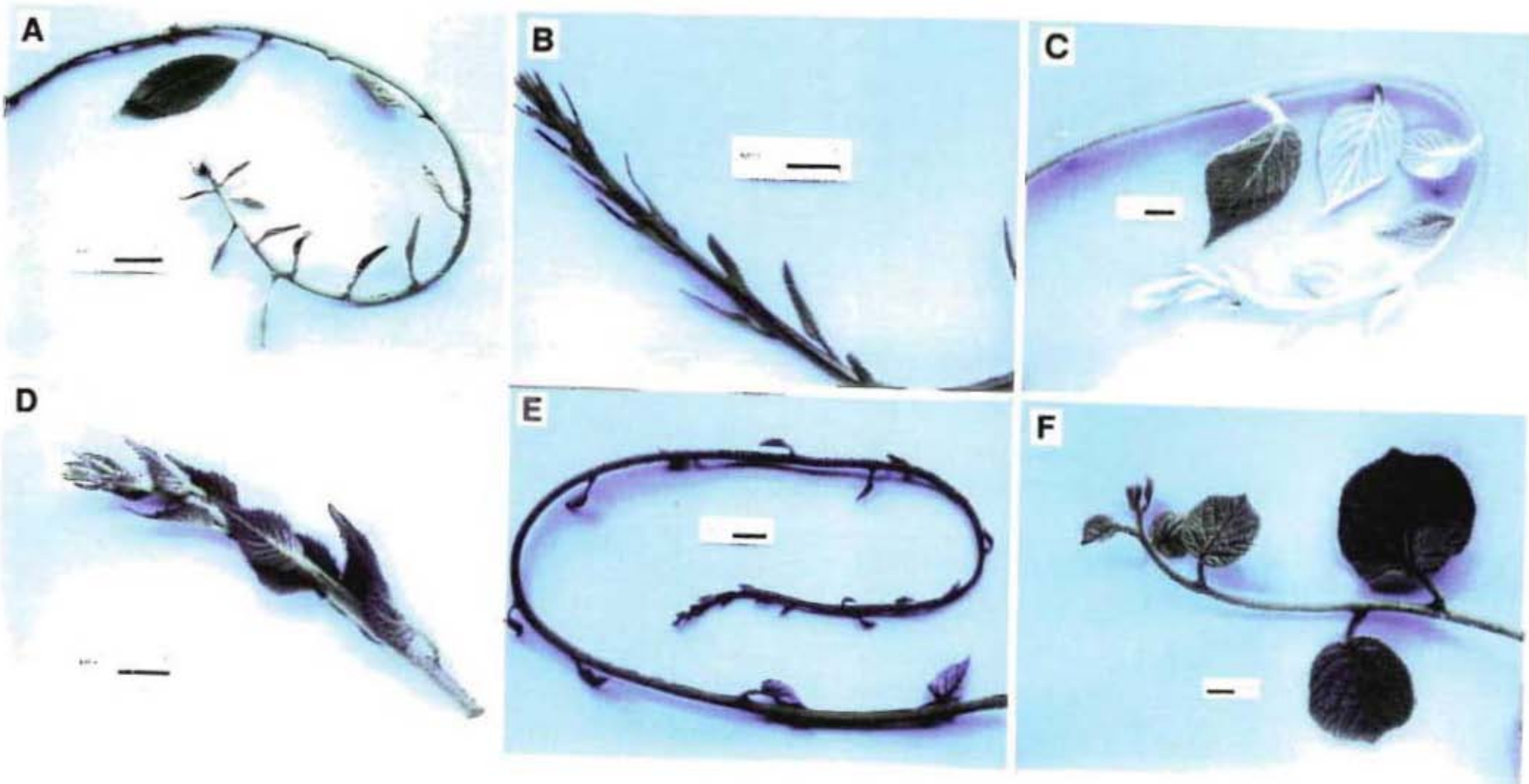

A
B
C
D
E
F

Table 2.5(a)

Juvenile Shoot Characters in some *Actinidia* Taxa

Taxon	distinguishing features of growth habit	young leaf shape[3]
A. arguta var. *arguta*	long "rat-tail" [1] shoots	lanceolate to narrowly trullate to ovate
A. arguta var. *cordifolia*	long "rat-tail" shoots	lanceolate to narrowly trullate to ovate
A. rufa	long "rat-tail" shoots, leaves point basipetally[1]	lanceolate ovate
A. melanandra var. *melanandra*		narrowly trullate ovate
A. *kolomikta*		lanceolate ovate
A. polygama		lanceolate ovate
A. valvata		lanceolate ovate
A. callosa var. *henryi*	many "rat-tail" shoots	ovate
A. chrysantha	long "rat-tail" shoots, leaves point basipetally	lanceolate
A. indochinensis	long "rat-tail" shoots, leaves point basipetally	lanceolate
A. melliana	shoots curl gently at the apex	lanceolate
A. hemsleyana var. *hemsleyana*		lanceolate
A. latifolia	long "rat-tail" shoots, leaves point basipetally	lanceolate ovate
A. eriantha		trullate to rhombic to elliptic ovate
A. chinensis var. *chinensis* 3/6/14b*	leaves point basipetally	very widely trullate to quadric rhombic to ovate
A. chinensis var. *chinensis* 460.4*	same	same
A. chinensis var. *chinensis* 460.9*	same	same
A. deliciosa var. *deliciosa* 'Hayward'		very widely trullate to quadric rhombic ovate
A. deliciosa var. *deliciosa* 'Matua'	shoots may curl and twist more than other cultivars of *A. deliciosa*	ovate to widely ovate
A. deliciosa var. *deliciosa* 'Bruno'		widely to very widely ovate
A. deliciosa var. *chlorocarpa*		ovate to very widely ovate

Continued .....

Footnote : * Numbers are different genotypes

Table 2.5 (b) Juvenile Shoot Characters in some *Actinidia* Taxa

Taxon	shoot colours (juvenile shoots)	hairs on young shoots: colour and persistence
A. arguta var. *arguta*	stem bright green pale green leaves with pink apices and margins	Fine, ginger white tomentum hairs lost 30-40 cm from apex. Older leaves polished.
A. arguta var. *cordifolia*	stem pale green pale green leaves with red margins	Fine, ginger coloured tomentum. Hairs lost 10-20 cm from apex. Older stems matt surface.
A. rufa	pale green leaves bronze margins & interveinal teeth bright green	Fine, dense, velvet-like, ginger tomentum. Hairs lost 30-40 cm from apex.
A. melanandra var. *melanandra*	stem red-brown leaves bright yellow-green red margins	Sparse, pale brown tomentum on leaf surfaces, stems polished glabrous.
A. kolomikta	young leaves bright red pink	Fine, pale brown tomentum on stems, youngest leaves with spiny transparent hairs near margins.
A. polygama	young stems including leaves bright green	Fine, pale brown tomentum on stems soon lost near apex, stems glossy, leaves finely tomentose.
A. valvata	young stems and leaves bright green	same as *A. polygama*
A. callosa var. *henryi*	young stems bright purple brown colour confined to vines with aging shoots	Bright rusty red tomentum on all shoot surfaces. Persistent tomentum in axils of of lateral leaf veins of leaf underside.
A. chrysantha	young leaves pale pale to lime green	Fine, ginger brown tomentum on all shoot surfaces. Hair-bases persistent on leaves, petioles, buds.
A. indochinensis	stems pale brown green to tan green (near apex) leaves pink to bronze above brown below	Fine ginger brown tomentum soon lost, leaves and stems polished.

Continued ....

Table 2.5 (b) Cont...

Juvenile Shoot Characters in some *Actinidia* Taxa

Taxon	shoot colours (juvenile shoots)	hairs on young shoots: colour and persistence
A. melliana	stem bright light green, younger leaves bronze near margins	Densely tomentose. Hairs coarse brillant red near apex fading to red-brown with age, hairs persistent.
A. hemsleyana var. *hemsleyana*	young stems and leaves pale green	Fine, dense, velvet-like, ginger tomentum. Long ginger-white hairs near petiole and abaxial veins.
A. latifolia	leaves and stems pale green	Fine, dense, velvet-like, pale brown tomentum soon lost near apex, underlying dense white hairs interveinal[4].
A. eriantha	shoots and leaves pale green overlain by milky-white (incanescent) hairs	Long, dense, milky-white tomentum, especially dense on lower surfaces. Hairs very persistent, surface "woolly".
A. chinensis var. *chinensis* 3/6/14b*	stem pale green but younger shoots bronze interveinally	Pale ginger brown hairs on shoot and leaf upper surface. Hairs ginger brown on petioles; underlying dense white hairs interveinal[4]. White (stellate) hairs only persist (abaxial).
A. chinensis var. *chinensis* 460.4*	same	same as 3/6/14b
A. chinensis var. *chinensis* 460.9*	same	same as 3/6/14b
A. deliciosa var. *deliciosa* 'Hayward'	shoots pale green brown red in sun	Long, ginger brown hairs restricted to veins, soon lost. Hairs ginger brown on petioles (very hairy); underlying dense white hairs interveinal[4], abaxial and persistent.
A. deliciosa var. *deliciosa* 'Matua'	similar to 'Hayward'	same as *A. deliciosa* 'Hayward'
A. deliciosa var. *deliciosa* 'Bruno'	similar to 'Hayward'	same as *A. deliciosa* 'Hayward'
A. deliciosa var. *chlorocarpa*	shoot green becoming near apex	Long, dense, bristly ginger hairs on shoots. Petioles thickly hairy. Young leaves dense adaxial cover of white hairs.

Footnotes:

[1] Long rat-tail described shape and overall shoot form characteristic of apical regions of shoot.

[2] Leaf apices of successive leaves along a cane all point toward the base of a shoot.

[3] Shape transition of young leaves described from apex to base, i.e. in a basipetal manner, after S.Y.S.T.A.N.Z (1962).

[4] Regarding *Stellatae*: white stellate hairs located on leaf underside are interveinal to primary and lateral (2°) veins.

* Numbers are different genotypes.

(Refs cited in table: a = Dilcher 1974; b = Hickey 1973, 1979; c = Stace 1965; d = Esau 1965; e = Isebrands and Larson1980)

TABLE 2.6: CRITERIA USED FOR CLASSIFYING LEAF VENATION

Type of vein	common name(s)	identification criteria/properties
Primary (1°) vein Refs a, b, c, e	major vein midrib medial vein	- continuous with the petiole - tapers in size from petiole to apex (if pinnate) - thickest vein(s) in leaf - usually most central vein - acropetal differentiation
Secondary (2°) vein Refs a, b, c	lateral vein "nerves" or "2° nerves"	- next thickness of class of veins below that of the 1° - decreases in thickness from centre toward margin of leaf - arise as branches from the 1° - acropetal differentiation
Intersecondary veins Refs a, b	none	- arise from the 1° vein - intermediate in thickness between 1° vein and 2° veins proper
Tertiary (3°) vein Refs a, b, c, d	crossbars	- arise from 1° or 2° veins - maintain constant thickness along their entire course - basipetal differentiation
Quaternary (4°) vein Refs a, b, c, d	areoles	- delimit smallest enclosed areas inside 3° veins and hence determine size of areoles - usually arise and branch at orthogonal angles - basipetal differentiation
Quinternary (5°) Sextenary (6°) veins Septenary (7°) Refs a, b, c	veinlets collectively "veinule reticulum"	- 5°, 6°, 7° are first, second and third orders of branching arising from the 4° veins - latter two form ultimate venation which is "blind-ending"

2.3.2 Leaf venation in some *Actinidia*

2.3.2.1 *Orders of leaf venation*

A basic tenet in classifying leaf venation is definition of the various orders of venation.

> The fundamental rule for determination of the order of a vein is its relative size at its point of origin. Where a lateral vein branch is approximately equal in width, measured just above the point of branching, to the continuation of the source vein just above the point of branching, both branches are of the same order; where the lateral vein branch is markedly finer than the continuation of its source, that branch is of a higher order.
>
> Hickey 1979, page 32.

Currently accepted criteria for defining and assigning orders of leaf venation are summarised in Table 2.6, with appropriate citation of sources.

In most cases orders of leaf venation can be identified with intuition and practice. There are, as Hickey *loc. cit.* asserts, problems in defining orders of venation, where primary veins branch near the leaf apex, or in cases where secondary veins ramify repeatedly near the margin of the leaf.

2.3.2.2 *Pectinal venation*

Spicer (1986) defined "pectinal veins" by the following criteria :

1. Basal lateral veins differing from main secondaries in the production of abmedial veins throughout their length; development of a greater number of abmedial branches than any other secondary veins.
2. Because of their comb-like appearance, these lateral (secondary) veins are termed pectinal veins, [from the Latin pecten = comb.]
3. Because pectinal veins support more abmedial branches than any other subsidiary of the midvein, there can only be one pair of pectinals per leaf. However in some palmately veined leaves several ranks of pectinal veins may be present.

   Spicer *loc. cit.* page 383

   Where more than one pair of pectinals is present, the pectinal with the smallest angle between its admedial side and the midvein is designated the α-pectinal and other pectinals are numbered basipetally.

4. Leaves with intermediate venation need only be described in terms of the overall observable characters and whether the pectinal veins are well or poorly developed in terms of the area of lamina that they or their branches serve.

Spicer *Loc. cit.*, page 383.

For further clarification of these points refer to Spicer (1980), especially Figure 1, page 381.

2.3.2.3 *Primary venation* (Table 2.7)

The primary vein in most *Actinidia* is straight in course and rarely curved, as in *A. melliana.*

The diameter of the primary vein in relation to the width of the blade (see Dilcher 1974, page 36), ranges in thickness from 0.7 - 2.0% in mature leaves of *Actinidia.* The diameter of the primary vein measured halfway along its length, is usually "weak" or "moderate" in size (Dilcher 1974, page 37), but is very rarely "stout" as in leaves of *A. deliciosa* var. *deliciosa* 'Bruno'.

Most *Leiocarpae* studied have much thinner primary veins with diameters less than or equal to 1% of the lamina width, except for *A. arguta* var. *arguta.* Several genotypes of *A. chinensis* var. *chinensis* have similar primary vein thicknesses of ca. 0.7% Three cultivars of *A. deliciosa viz:* var. chlorocarpa; vars deliciosa 'Matua' and 'Hayward', have primary vein thickness ranging from 1.3-1.5%.

2.3.2.4 *Secondary venation* (Table 2.7)

The angle of divergence (a.o.d.) of the secondary vein from the primary vein is consistently moderate (45-65°, Dilcher 1974, page 38). The a.o.d. of the secondary veins is uniform, except in leaves with pectinal veins (see Section 2.3.2.2).

The transition between different types of venation (Hickey 1979, page 30; Figure 4.3) is not always discrete. For instance, the laterals or secondary veins of most *Actinidia* do not form obviously arched anastomoses with vertically adjacent secondaries, however, they do form parietal cross-connections of a curved to orthogonal nature, near the margin. The behaviour of distally branching secondary veins of most *Actinidia* is semicraspedodromous:

....semicraspedodromous: secondary veins branching just within the margin, one of the branches terminating at the margin, the other joining the super adjacent secondary...

Hickey 1979, page 30.

Semicraspedodromous venation is seen in the leaves of *Actinidia* examined from the *Leiocarpae, Maculatae* and *Strigosae.*

Leaves of the *Stellatae* have secondary veins which are termed craspedodromous :

> ...Craspedodromous: secondary veins terminating at the margin.
> (1) Simple: all of the secondary veins and their branches terminating at the margin.
>
> Hickey 1979, page 30.

The relative thickness of the secondary veins is "moderate" compared to that of the primary vein in *Leiocarpae* and *Stellatae* leaves, but is noticeably more "fine and hair-like" in the *Maculatae* and *Strigosae.*

Intersecondary veins are rare or absent in the leaves of most *Actinidia* examined, but they are more frequent in leaves whose secondary veins are spaced widely apart, e.g. *A. melliana* (Figure 2.8) and *A. deliciosa* var. *deliciosa* 'Bruno'; *A. chinensis* var. *chinensis* (Figure 2.11).

2.3.2.5 *Tertiary venation* (Table 2.7)

Tertiary veins are numerous, well-developed and are an obvious feature of all *Actinidia* seen. The angle of the tertiary veins increases in relation to the primary vein, from the apex to the leaf base. Tertiary veins are classified as "markedly" or "rigidly" percurrent, in that, they arise from and join with vertically opposite secondary veins. They are usually simple with few being forked (Dilcher 1974, pages 563, 565). The central region of each tertiary vein is distended convexly in an abmedial direction (away from the midrib). Each tertiary vein arises from the lower or abmedial side of the secondary vein at an acute angle and rejoins the nearest secondary vein at a right angle, on the admedial or upper side of that secondary. Tertiary veins occur in pairs in relation to the secondary veins and their arrangement may be predominantly opposite, alternate or both may occur in equal proportions (Dilcher 1974, page 48). The intertertiary veinal distance may be $\geqslant$ 0.5 cm or $\leqslant$ 0.5 cm.

2.3.2.6 *Basal venation in Actinidia leaves*

Basal venation shows a range of complexity within the *Actinidia* studied (see Table 2.7).

Basal secondary veins may be morphologically indistinguishable from other secondary veins as in *A. melliana* (Figure 3.5) and *A. hemsleyana.* In these cases,

the lowermost secondary veins emerge from the primary vein in a normal manner and pectinal veins are absent.

Other taxa such as *A. melanandra* and *A. callosa* var. *henryi* have leaves with the earliest signs of specialisation of basal veins; that is "weak" or diminutive pectinals, where the lowermost secondary veins are poorly differentiated from super adjacent secondary veins and the pectinal veins occupy a small percentage of the lamina area.

Stellatae leaves show a full transition from weak pectinals, e.g. *A. latifolia* (Figure 3.7), to weak pectinals with super adjacent transitional pectinals, as seen in *A. chinensis* var. *chinensis* (Figure 3.10). The series culminates in *A. deliciosa* (Figures 3.11, 3.12), where transitional pectinals and "pectinals proper" become well-developed and may occupy a considerable area of the lamina.

Leaves of the *Stellatae* have the most intricate pectinal venation, especially those of *A. deliciosa* - the commercial kiwifruit and related taxa. In a typical kiwifruit leaf (*A. deliciosa* 'Hayward'), the lowermost secondary vein emerging from the primary vein (midrib), usually with a branching angle 90°, is termed the "α-pectinal" (Figures 3.11, 3.12). Immediately below this vein, a smaller pectinal termed the "β-pectinal" arises, either from the same, or at a lower point along the primary vein. α-pectinal veins appear to support another order of branching analogous to tertiary veins, the so-called medial veins. As these are oriented "away from" (= ab) the centre of the leaf, they are termed abmedial veins (Spicer 1980). Each α-pectinal in *A. deliciosa* is associated with 6-8 α-abmedials of 10-20 mm in length (Figure 3.12). β-pectinal veins have 2-3 β abmedial veins, which are associated with another order of pectinals which branch "toward the centre" and are hence termed admedial veins.

Transitional pectinals are those secondary veins which have some, but not all of the characteristics of pectinal veins. These are transitional veins because their comb-like behaviour is confined to the distal region of the parent vein only, whereas, true pectinal veins branch to produce medial veins along their entire length. Transitional pectinal veins can occupy a considerable area of the lamina in plants such as *A. deliciosa* var. *chlorocarpa.*

TABLE 2.7 COMPARISON OF SELECTED LEAF VENATION CHARACTERS
(Based on Dilcher 1974)

Taxon	Type of venation Pinnate;	Primary vein: thickness[1]	course	Variations in angle of divergence of 2° veins from the 1° vein
A. arguta var. *arguta*	semicraspedodromous	2.03%,	moderate, straight	uniform
A. arguta var. *cordifolia*	semicraspedodromous	0.83%,	weak, straight	uniform except pectinal
A. rufa	semicraspedodromous	0.95%,	weak markedly curved	curved uniformly
A. melanandra var. *melanandra*	semicraspedodromous	1.20%,	weak, straight	uniform
A. kolomikta	semicraspedodromous	1.00%,	weak, straight	upper and lower more obtuse
A. polygama	semicraspedodromous	0.70%,	weak, straight	curved uniformly
A. valvata	semicraspedodromous	0.60%,	weak, straight	uniform
A. callosa var. *henryi*	semicraspedodromous	0.70-1.00%,	moderate, straight	uniform
A. chrysantha	semicraspedodromous	1.17%,	weak, straight	uniform
A. indochinensis	semicraspedodromous	2.03%,	moderate, straight	uniform
A. melliana	semicraspedodromous	1.04%,	weak, straight	uniform
A. hemsleyana var. *hemsleyana*	semicraspedodromous	1.96%,	moderate, straight	uniform
A. latifolia	craspedodromous simple	0.76%,	weak, straight	upper more acute than lower
A. eriantha	craspedodromous simple	1.66%,	moderate, straight	uniform
A. chinensis var. *chinensis* 3/6/14b*	craspedodromous simple	0.70%,	weak, straight	uniform except pectinals
A. chinensis var. *chinensis* 460/4*	craspedodromous simple	1.00%,	weak, straight	uniform except pectinals
A. chinensis var. *chinensis* 460/9*	craspedodromous simple	0.76%,	weak, straight	uniform except pectinals
A. deliciosa var. *deliciosa* 'Bruno'	craspedodromous simple	2.58%,	stout, straight	uniform except pectinals
A. deliciosa var. *deliciosa* 'Hayward'	craspedodromous simple	1.42%,	moderate, straight	uniform except pectinals
A. deliciosa var. *deliciosa* 'Matua'	craspedodromous simple	1.37%,	moderate, straight	uniform except pectinals
A. deliciosa var. *chlorocarpa*	craspedodromous simple	1.29%,	moderate, straight	uniform except pectinals

Footnote: * numbers are different genotypes

TABLE 2.7 (continued)

Taxon	Thickness of 2° veins relative to 1° veins	Distance between 3° veins (close, distant)	Contact angle[2] of 3° with 2° veins abmedial admedial
A. arguta var. *arguta*	moderate	close	45° (AR) 90°
A. arguta var. *cordifolia*	moderate	close	45° (AR) 90°
A. rufa	moderate	close	45° (AR) 90°
A. melanandra var. *melanandra*	fine and hair-like	distant	45° (AR) 90°
A. kolomikta	moderate	distant	80° (RR) 80°
A. polygama	moderate	distant	45° (AR) 90°
A. valvata	moderate	close	45° (AR) 90°
A. callosa var. *henryi*	fine and hair-like	close	45° (AR) 90°
A. chrysantha	fine and hair-like	close	45° (AR) 90°
A. indochinensis	fine and hair-like	close	45° (AR) 90°
A. melliana	fine and hair-like	distant	80° (RR) 90°
A. hemsleyana var. *hemsleyana*	fine and hair-like	distant	45° (AR) 90°
A. latifolia	moderate	close	45° (AR) 90°
A. eriantha	moderate	distant	45° (AR) 90°
A. chinensis var. *chinensis* 3/6/14b*	moderate	close	45° (AR) 90°
A. chinensis var. *chinensis* 460/4*	moderate	close	45° (AR) 90°
A. chinensis var. *chinensis* 460/9*	moderate	close	45° (AR) 90°
A. deliciosa var. *deliciosa* 'Bruno'	moderate	distant	45° (AR) 90°
A. deliciosa var. *deliciosa* 'Hayward'	moderate	distant	45° (AR) 90°
A. deliciosa var. *deliciosa* 'Matua'	moderate	close	45° (AR) 90°
A. deliciosa var. *chlorocarpa*	moderate	distant	45° (AR) 90°

Footnotes: 1. primary vein thickness = diameter expressed as a percentage of lamina width (maximal) 2. A = acute; R = right angles (a calculated value)

* numbers are different genotypes

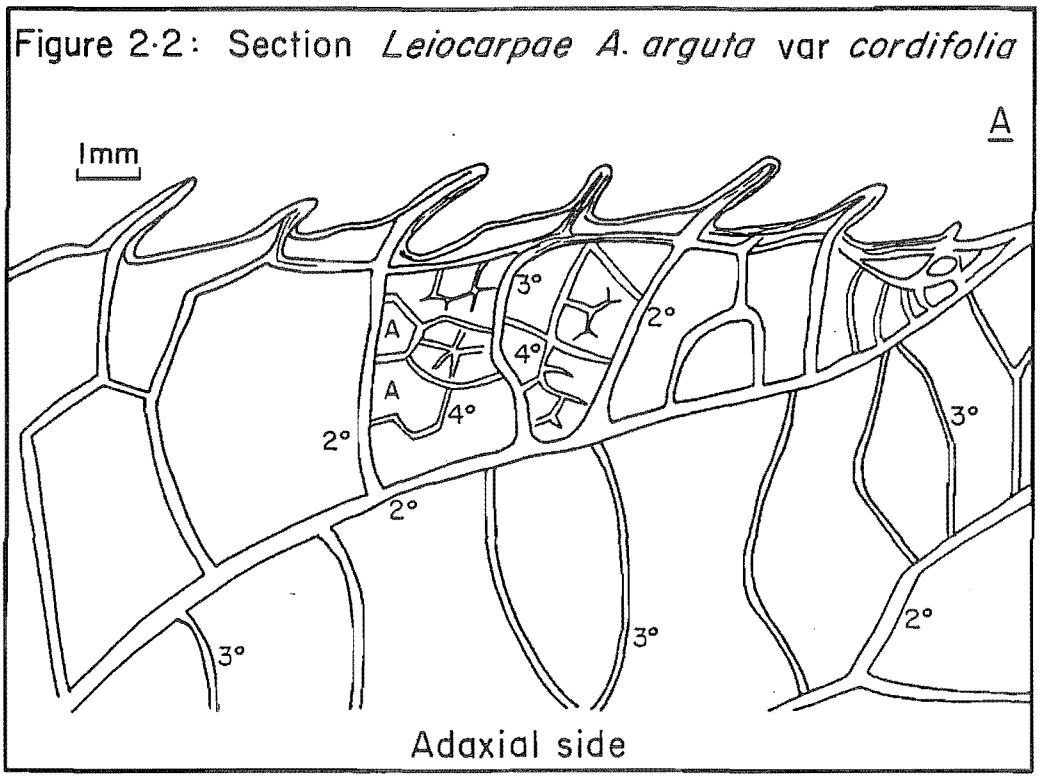
2.3.2.7 *Areolation and ultimate venation*

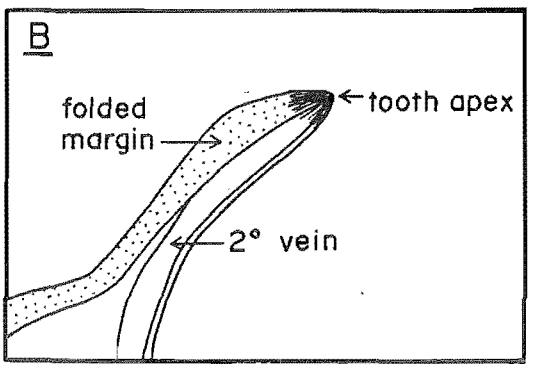
The higher or ultimate levels of leaf venation appear insignificant in scale, compared with other levels of venation. Despite appearances, these higher veins are pivotal in plant water-relations, as their fine-diameter tracheids are the main unloading points in the vascular pathway.

Areoles can be defined as :

> the smallest areas of the leaf tissue surrounded by veins which taken together form a contiguous field over most of the area of the leaf.
>
> Dilcher 1974, page 50.

Figure 2·2: Section *Leiocarpae A. arguta* var *cordifolia*





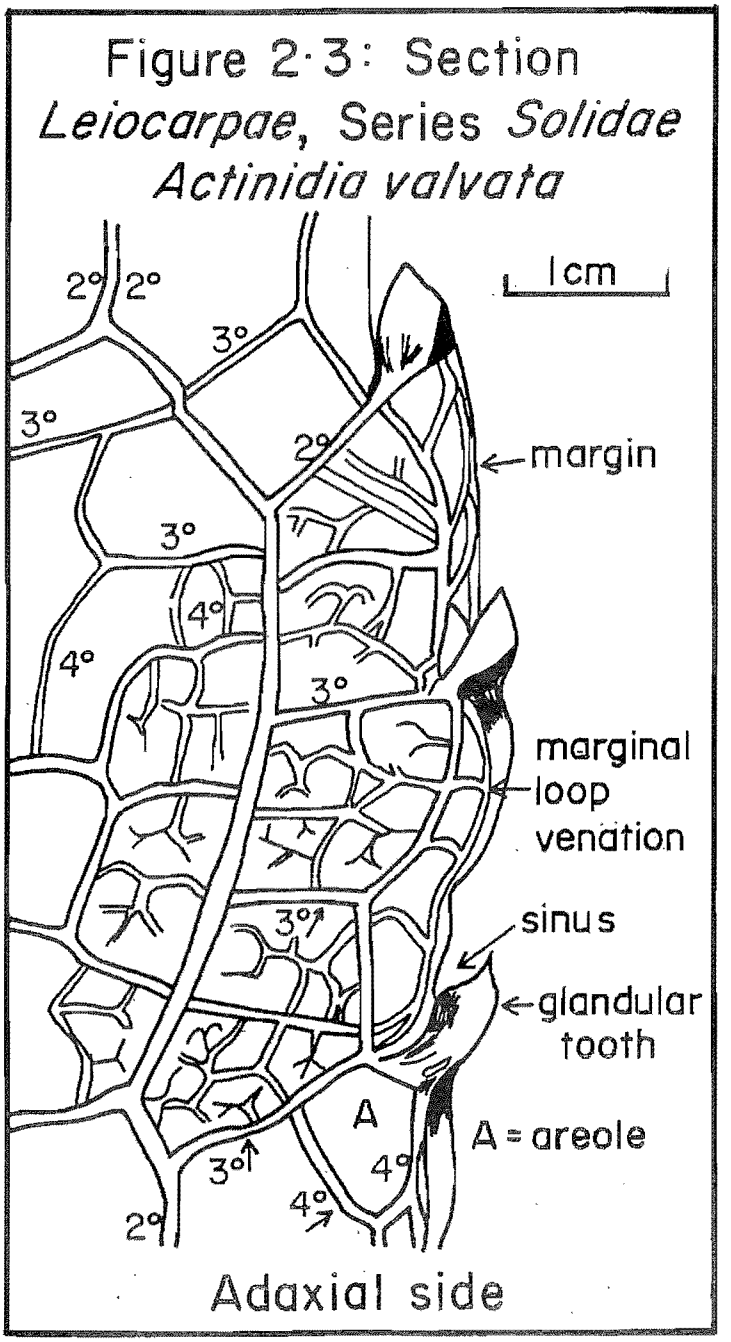
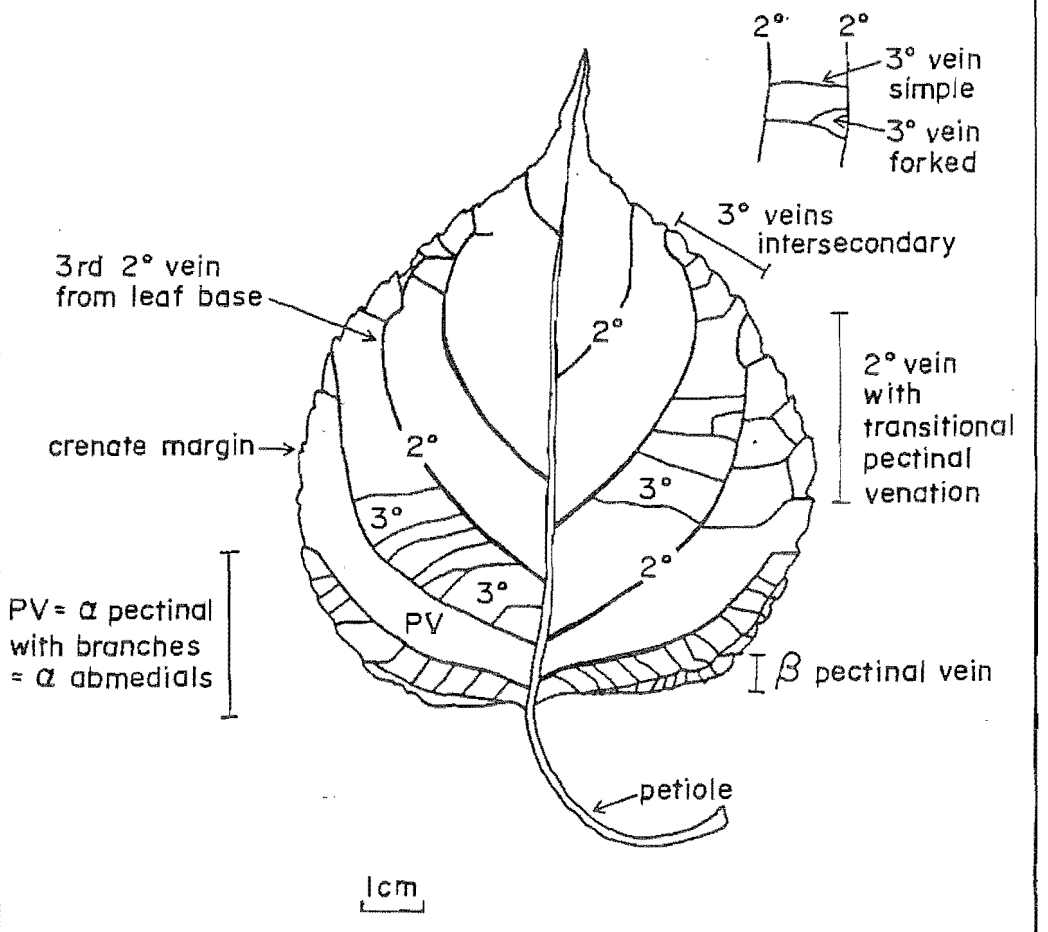


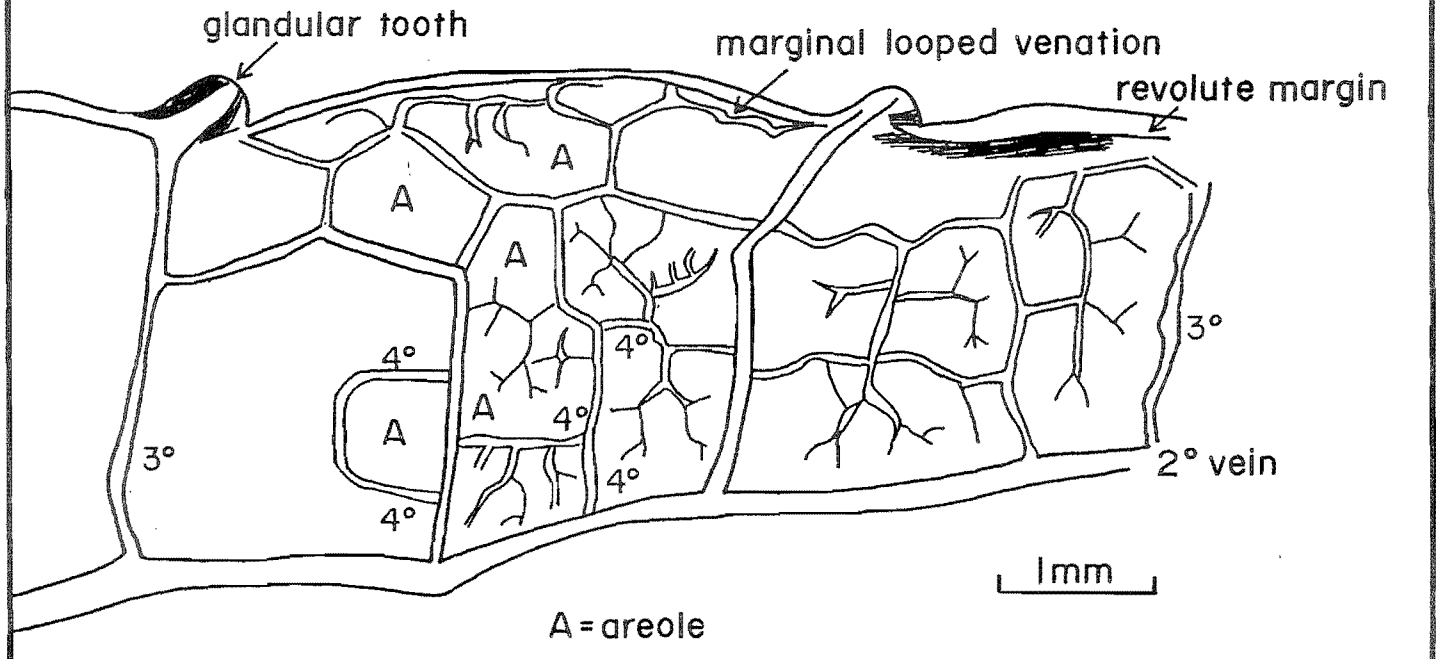
Figure 2·3: Section
Leiocarpae, Series Solidae
Actinidia valvata
1cm
2°
2°
3°
3°
2°
3°
4°
4°
3°
3°
margin
marginal
loop
venation
sinus
glandular
tooth
A
A = areole
3°
4°
2°
4°
Adaxial side

Figure 2·4 Section *Leiocarpae*
Series *Solidae*, *Actinidia valvata*



2° = secondary vein 3° = tertiary vein

Figure 2·5: Section *Maculatae*, *A. chrysantha*



Abaxial surface

Figure 2·6 : Section
Strigosae, Actinidia melliana

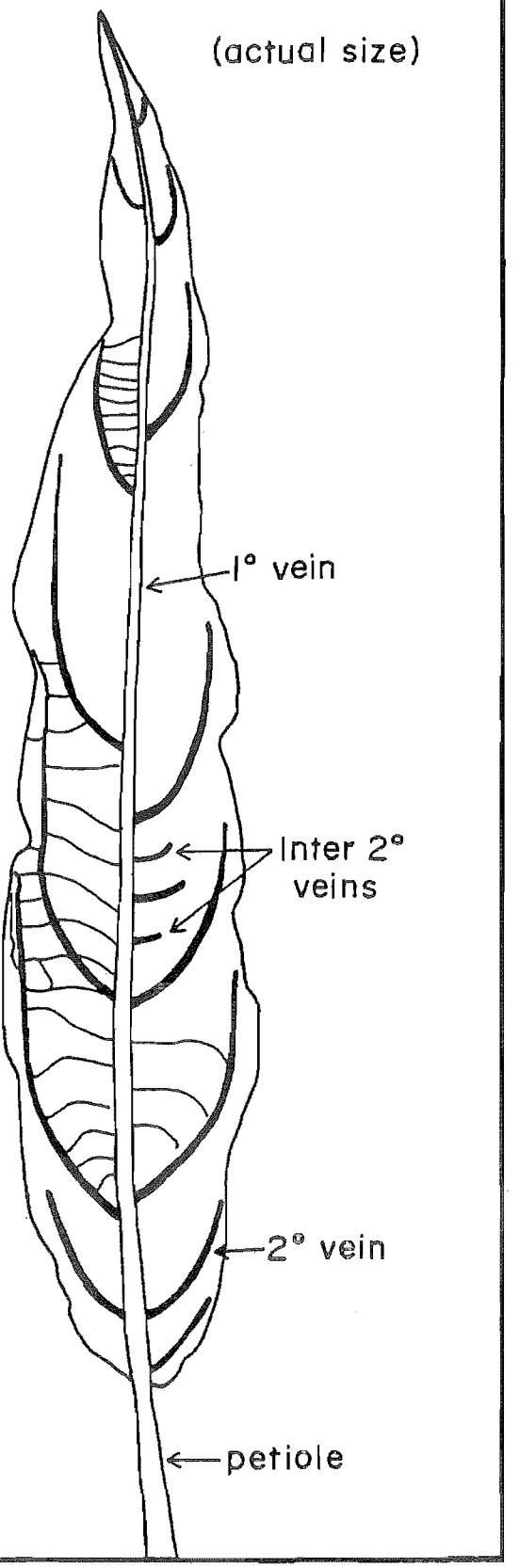


Figure 2·7: Section *Strigosae, Actinidia hemsleyana*

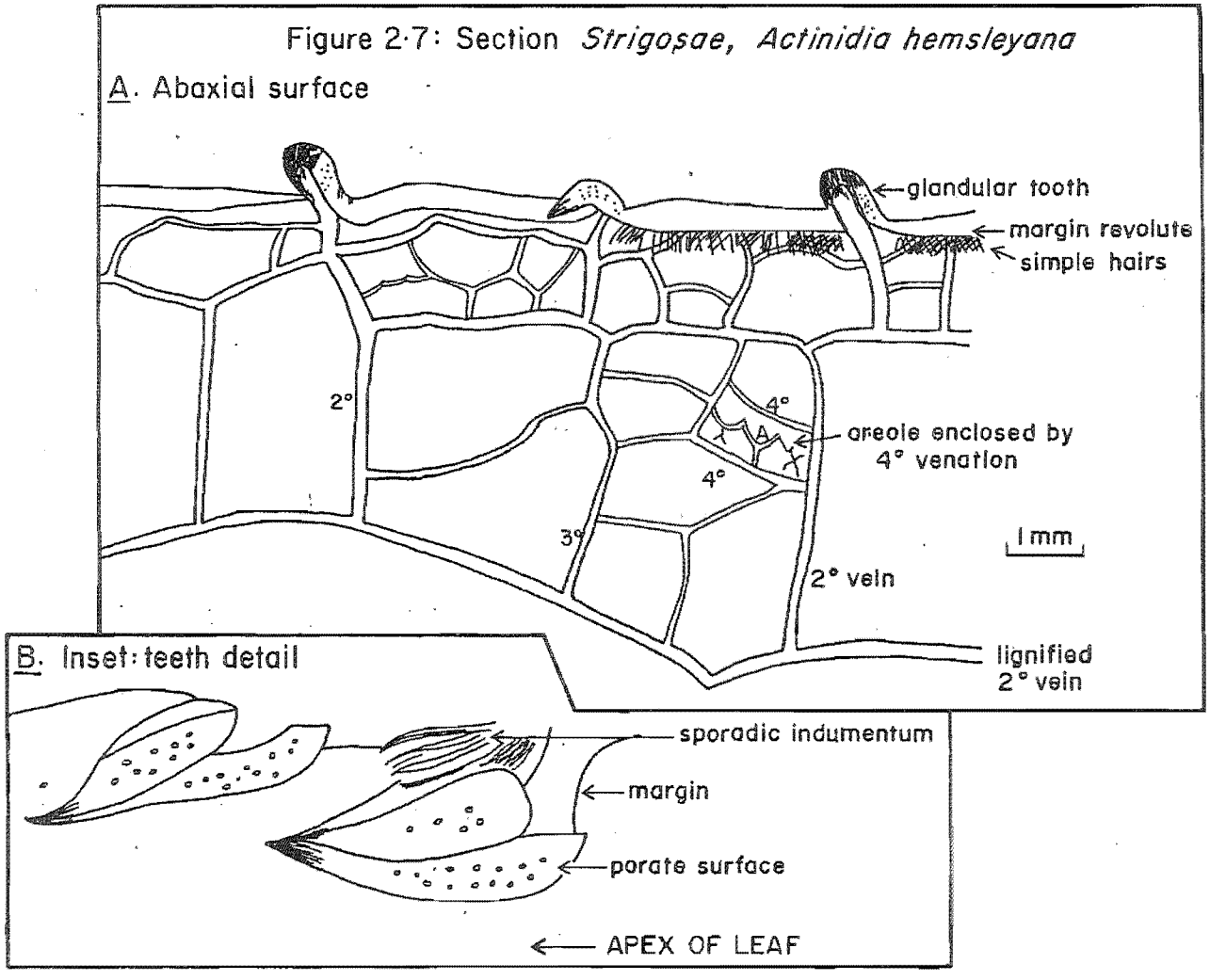


Figure 2·8 : Section *Stellatae*, *Actinidia latifolia*

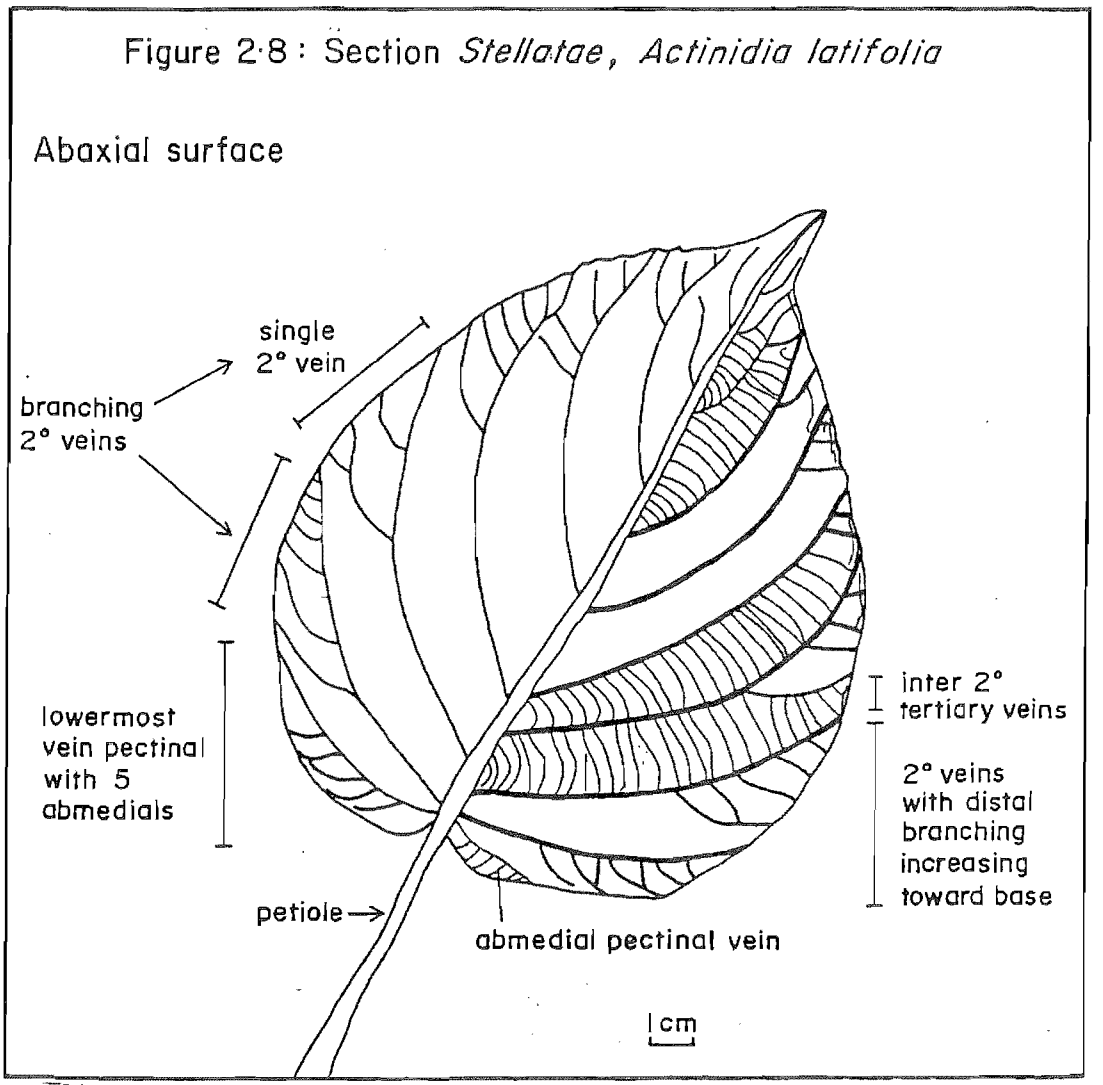


Figure 2·9: Section *Stellatae*, *Actinidia eriantha*

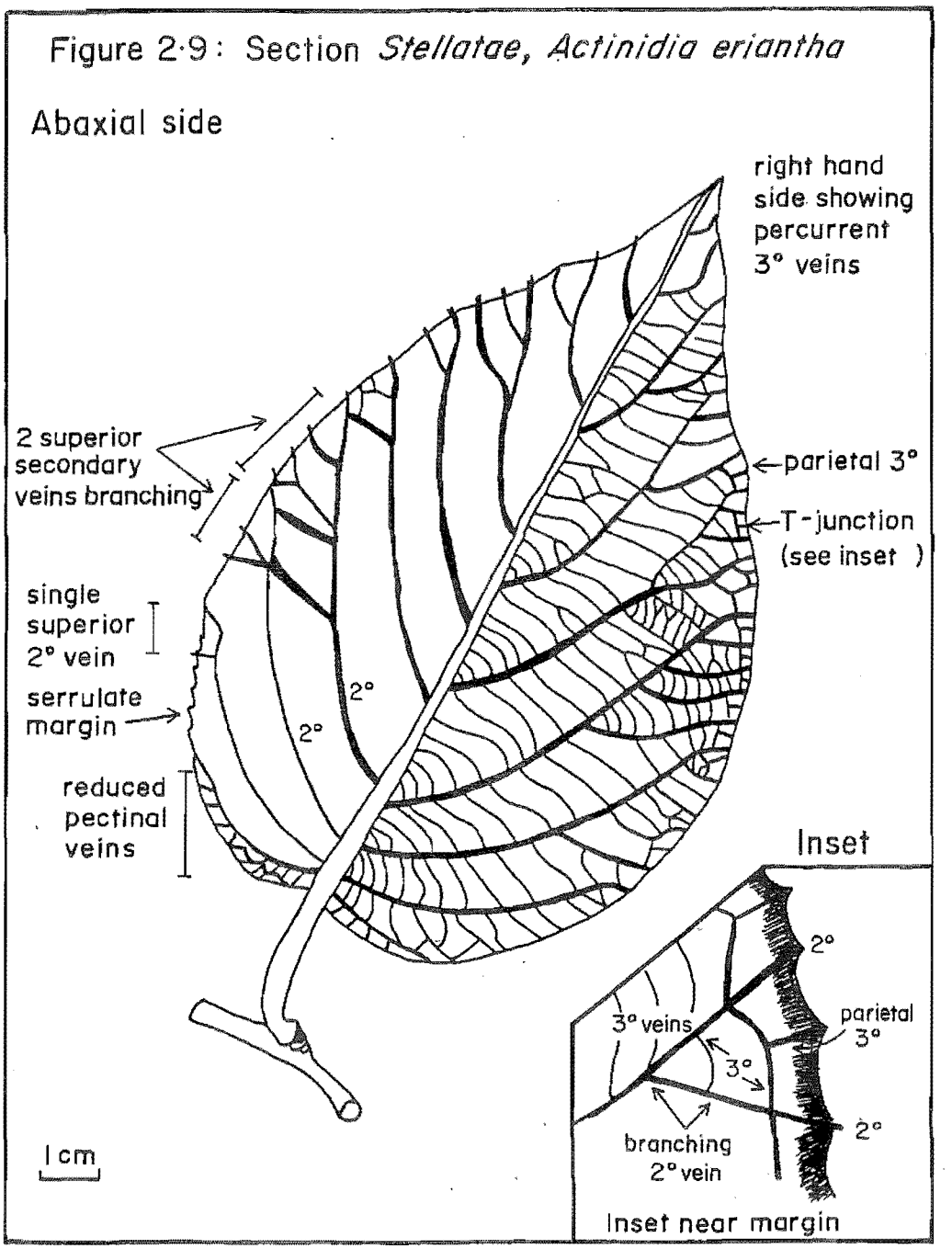
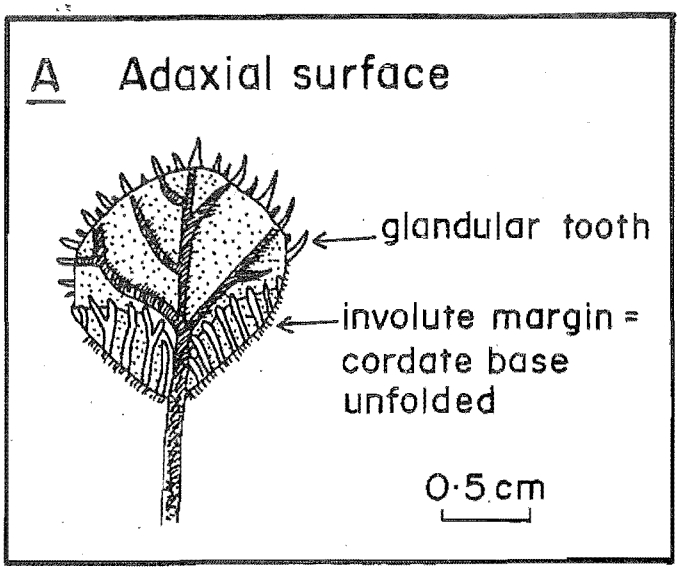


Figure 2·10: Section *Stellatae*, *Actinidia chinensis* var *chinensis*



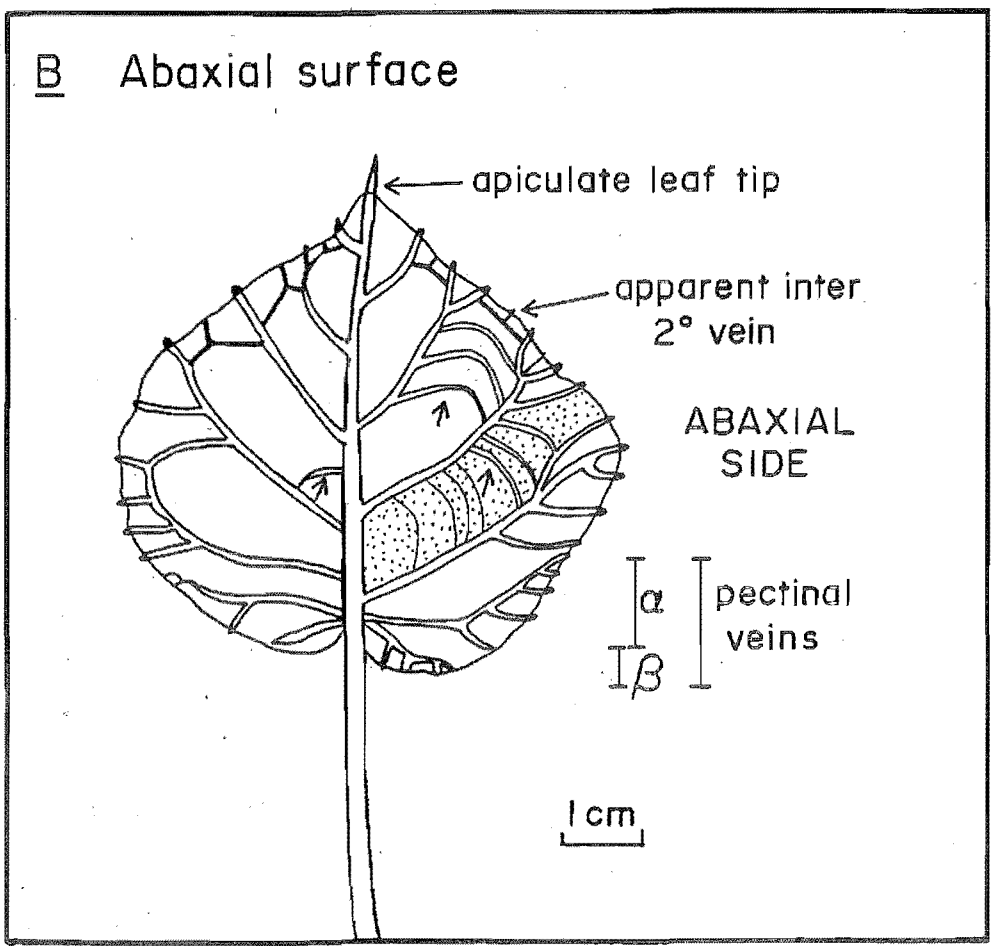


Figure 2·11:: Section *Stellatae*, *A. chinensis* var *chinensis*

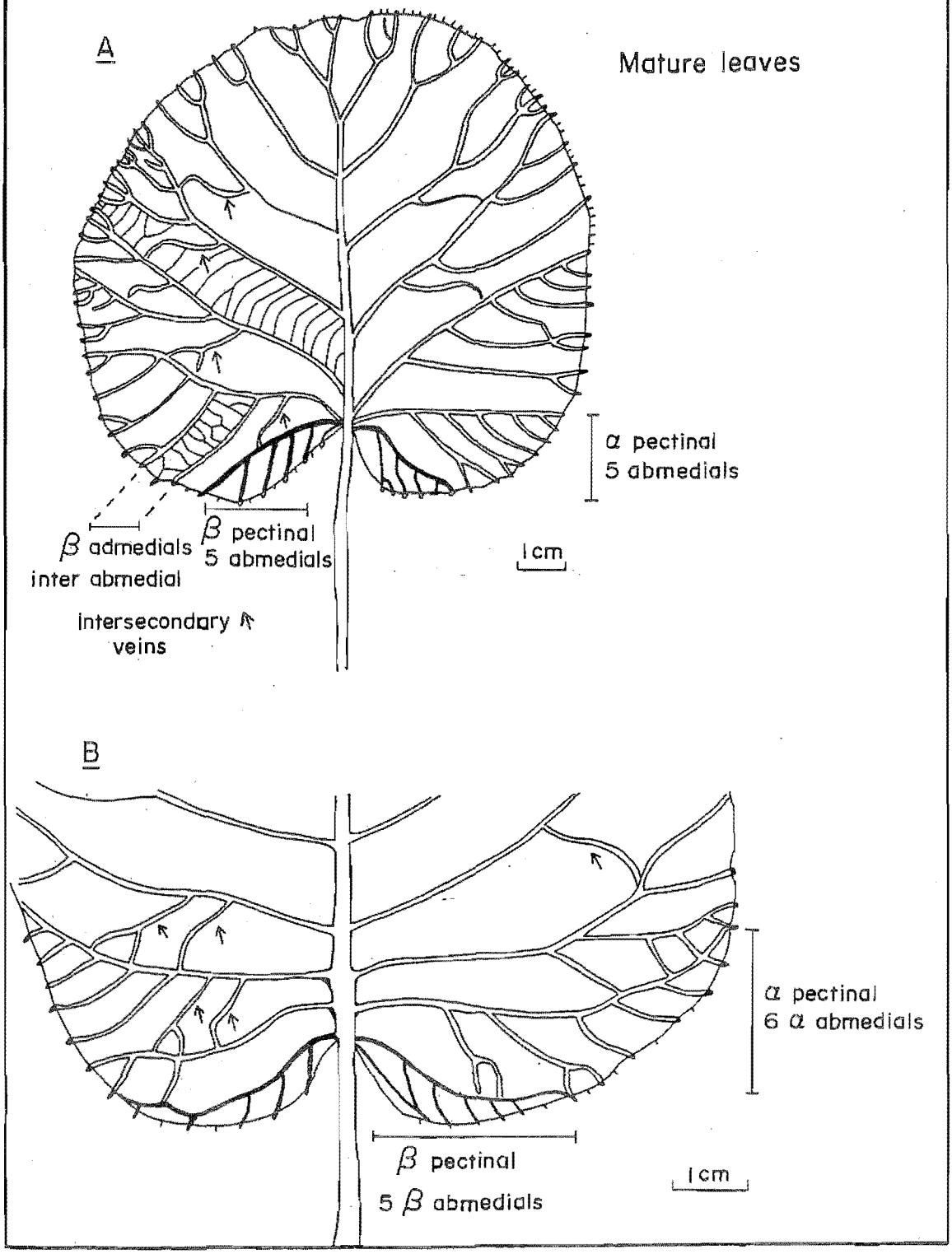
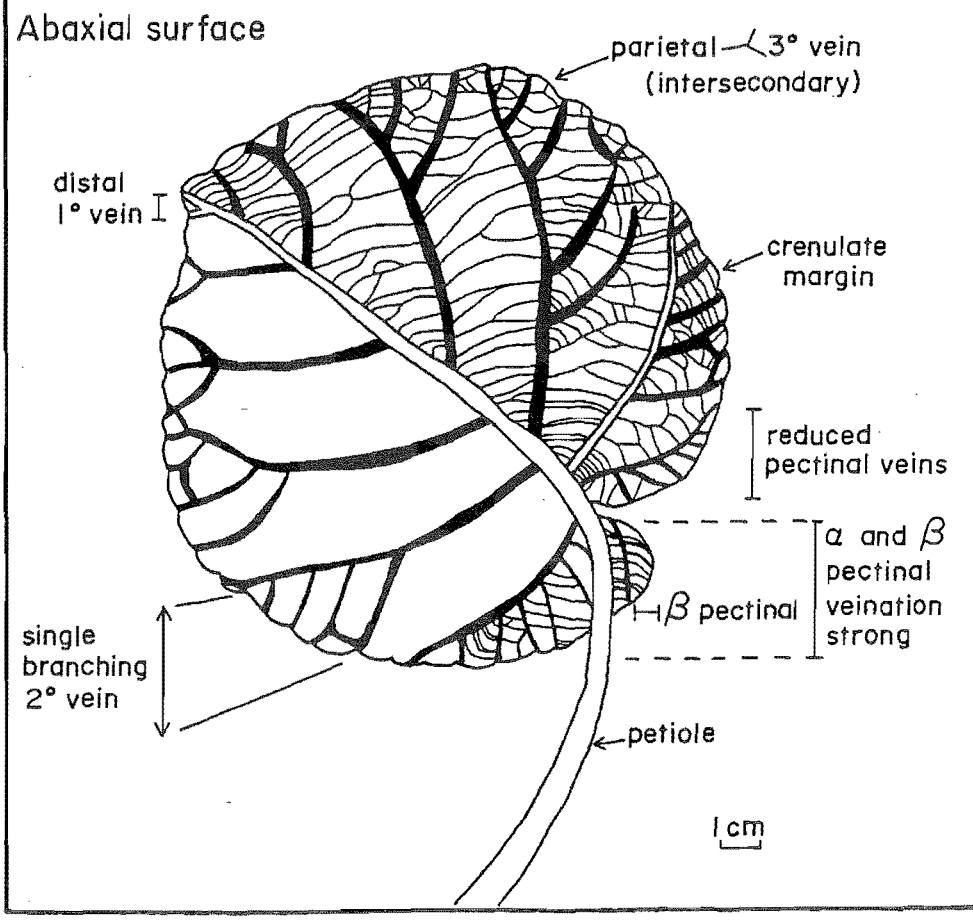


Figure 2·12: Section *Stellatae*
A deliciosa var *deliciosa* 'Hayward'



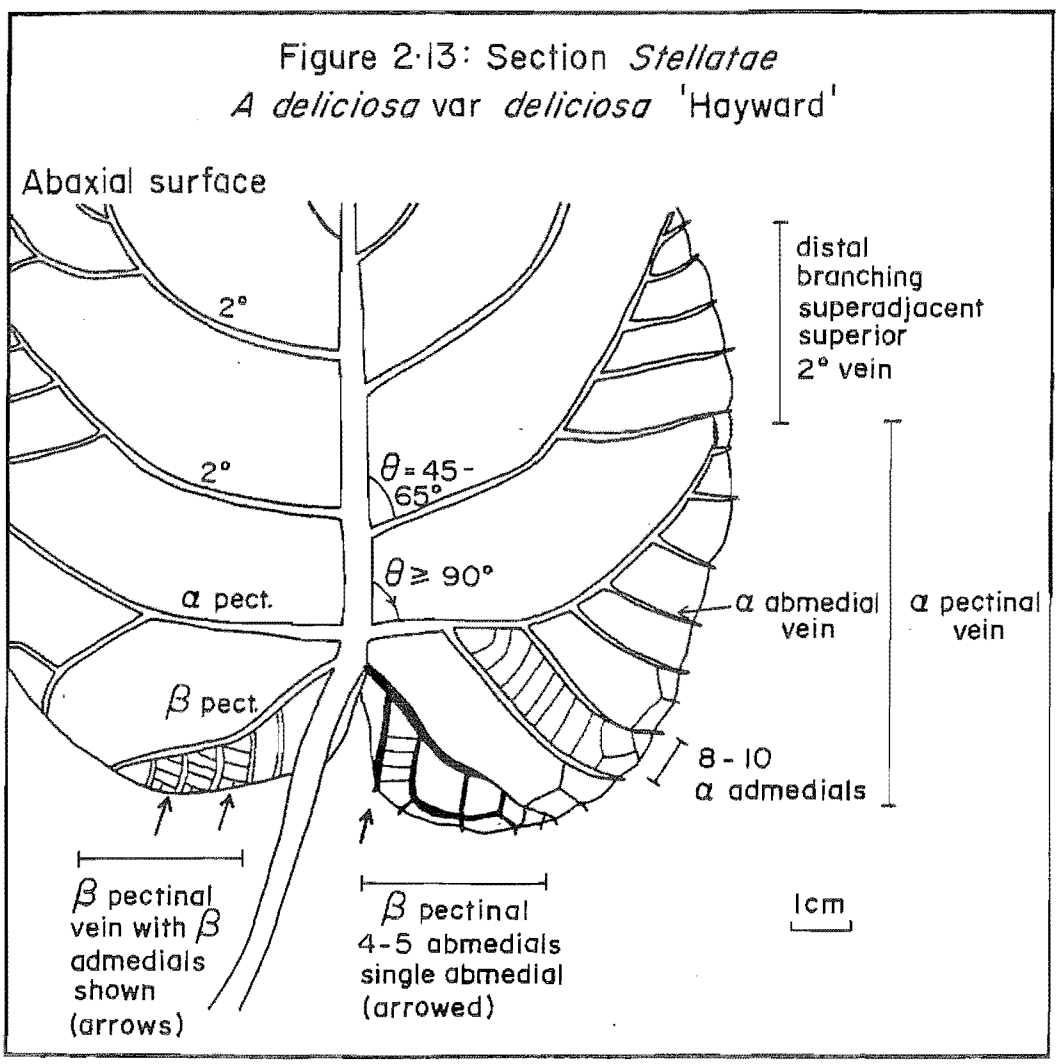


Figure 2·13: Section *Stellatae*
A deliciosa var *deliciosa* 'Hayward'

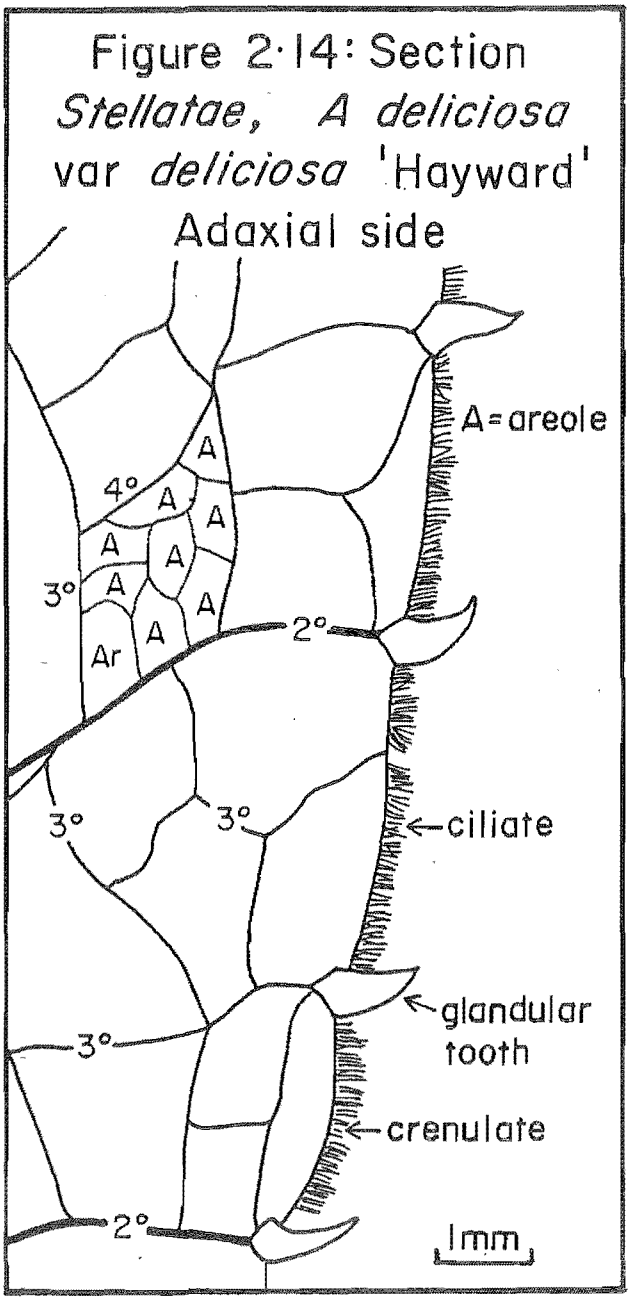
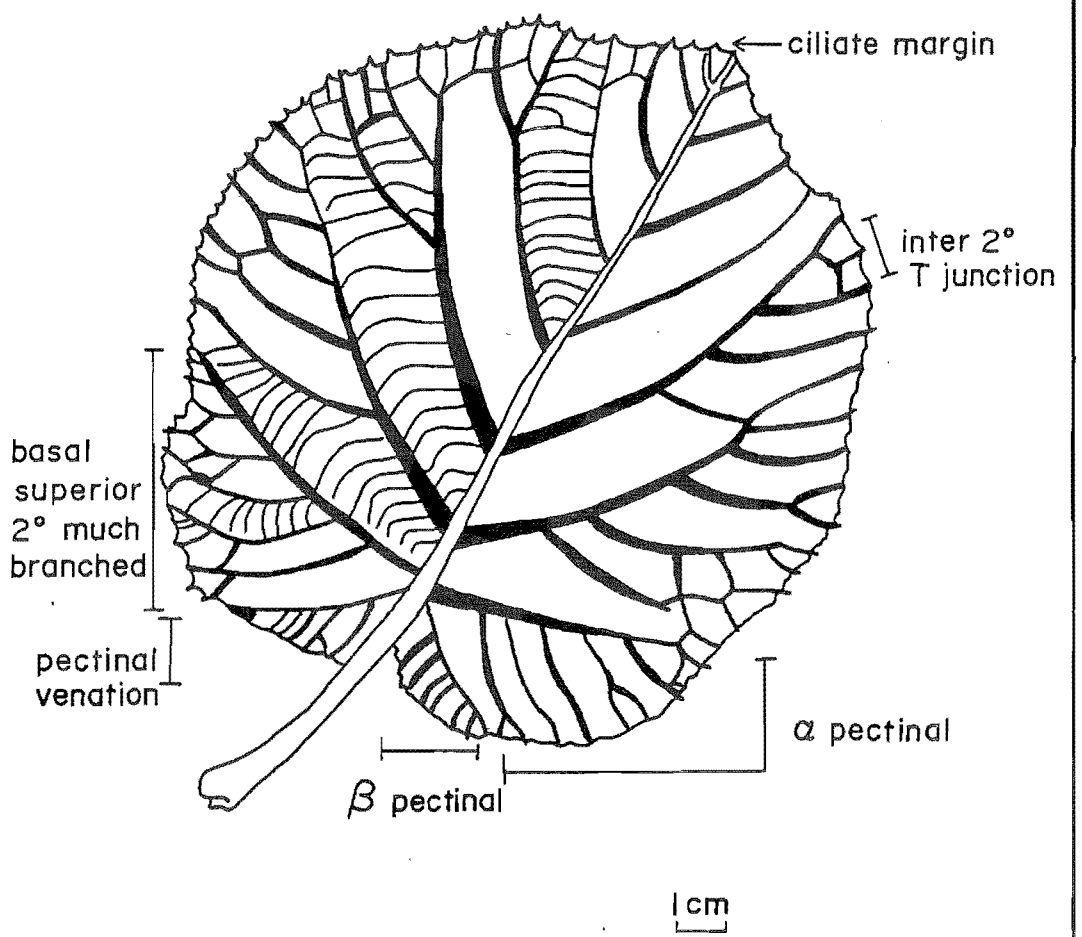


Figure 2·14: Section
Stellatae, A deliciosa
var deliciosa 'Hayward'
Adaxial side
A=areole
4°
3°
2°
A
Ar
3°
3°
ciliate
glandular
tooth
3°
crenulate
2°
1mm

Figure 2·15: Section *Stellatae*
Actinidia deliciosa var *chlorocarpa*



Areoles are typically bounded by quaternary veins which act as a buffer between the blind-ending veinlets and the closed continuum of primary, secondary and tertiary venation. The other system of closed venation in the plant, analogous to areoles, is proximal to the margin and is termed the parietal network of "loop-forming" veins. Terminology for ultimate venation is well-illustrated in Dilcher (1974) and Hickey (1979) and is otherwise self-explanatory.

The areoles of *Actinidia* leaves are regularly oriented with respect to secondary and tertiary venation. They are circumscribed by quaternary veins which arise and branch at orthogonal angles.

Higher orders of venation branch repeatedly within the areole (e.g. Plate 2.3) forming a ramified network of veinlets, which terminate in the leaf parenchyma. Quinternary (5^{o}) veins arise at right angles to the areole (4^{o} veins) and these support one or two further levels of branching termed sextenary (6^{o}) and septenary (7^{o}) veins, respectively. Sextenary veins originate from 5^{o} veins at acute angles and subtend this angle along their length. They usually branch in a similar fashion to form the ultimate level of venation, that is, 7^{o} venation.

Other criteria associated with areolation in *Actinidia*, which may be of taxonomic or physiological significance include : degree of areole development, areole shape; areole size and the frequency of veinlet branching. Some of these findings are summarised in Table 2.8 according to the categories of Dilcher (1974).

Assessment of areolation based on Dilcher *loc. cit.* is subjective. Hickey defined :

> regular areoles as those whose meshes are of relatively consistent shape and size.
>
> Hickey 1979, page 36.

Areoles of the *Stellatae* are "irregular to well-developed" as areole size and shape can be variable due to incomplete closure of the areoles by quaternary venation (see also Gao 1988).

Areoles of *Actinidia* are mainly quadrangular and pentagonal in form and are rarely if at all, triangular. Pentagonal areoles are increasingly common in advanced sections of the genus, e.g. *Stellatae*. The density of areolation, as estimated by maximal areole diameter, increases in members of the *Stellatae*, all of which have leaves with consistently medium sized (0.3-1 mm diam.), rather than large areoles (1-2 mm diam.) as in most *Actinidia*.

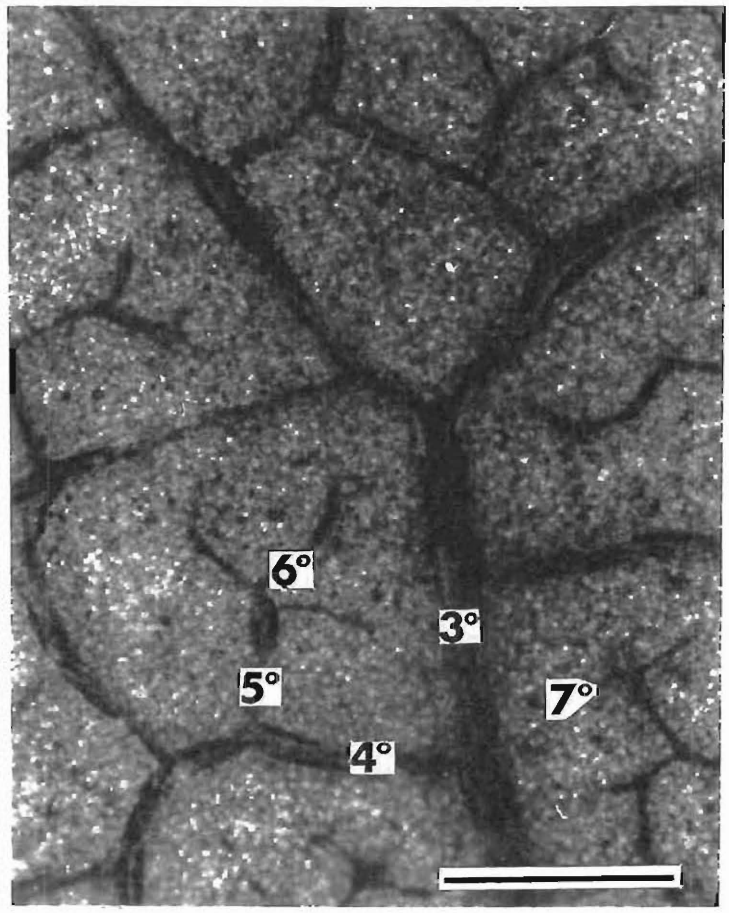


PLATE 2.3

"Semi-cleared" leaf of *A. valvata* revealing areolation.

Orders of venation: 3^{O} = tertiary, 4^{O} = quaternary; 5^{O} = quinternary, 6^{O} = sextenary, 7^{O} = septenary.
Areole delimited by 4^{O} venation (mostly).
Bar scale = 0.5 mm

TABLE 2.8 COMPARATIVE FORM OF AREOLATION IN LEAVES OF SOME *ACTINIDIA*

Taxon	areole development	areole shape(s)	areole size	veinlet branch number
A. arguta var. *arguta*	imperfect to well-developed	mostly pentagonal occasionally quadrangular	> 2 mm, very large	three times
A. arguta var. *cordifolia*	imperfect to well-developed	mostly pentagonal occasionally quadrangular	1-2 mm, large	twice
A. rufa	imperfect	quadrangular and pentagonal	1-2 mm, large	twice
A. melanandra var. *melanandra*	imperfect	quadrangular and pentagonal	1-2 mm, large	twice
A. kolomikta	imperfect	pentagonal	< 1 mm, medium	twice
A. polygama	imperfect	quadrangular and pentagonal	1-2 mm, large	three times
A. valvata	imperfect	quadrangular and pentagonal	1-2 mm, large	twice
A. callosa var. *henryi*	imperfect	quadrangular and pentagonal	0.3-1 mm, medium	twice
A. chrysantha	imperfect	quadrangular and pentagonal	1-2 mm, large	three times
A. indochinensis	imperfect	mostly pentagonal occasionally quadrangular	up to 1 mm, medium	twice
A. melliana	imperfect	variable: pentagonal quadrangular polygonal	1-2 mm, large	three times
A. hemsleyana var. *hemsleyana*	imperfect	quadrangular and pentagonal	1-2 mm, large	three times
A. latifolia	imperfect to well-developed	mostly pentagonal occasionally quadrangular	< 1 mm, medium	twice

TABLE 2.8 (continued)

A. eriantha	imperfect to well-developed	quadrangular and pentagonal	< 1 mm, medium	twice
A. chinensis var. *chinensis* 3/6/14b*	imperfect to well-developed	quadrangular and pentagonal	0.3-1 mm, medium	three times
A. chinensis var. *chinensis* 460/4*	imperfect to well-developed	quadrangular and pentagonal	0.3-1 mm, medium	twice
A. chinensis var. *chinensis* 460/9*	imperfect to well-developed	quadrangular and pentagonal	0.3-1 mm, medium	twice
A. deliciosa var. *deliciosa* 'Bruno'	imperfect to well-developed	mostly pentagonal occasionally quadrangular	0.3-1 mm, medium	twice
A. deliciosa var. *deliciosa* 'Hayward'	imperfect to well-developed	mostly pentagonal occasionally quadrangular	1-2 mm, large	three times
A. deliciosa var. *deliciosa* 'Matua'	imperfect to well-developed	mostly pentagonal occasionally quadrangular	0.3-1 mm, medium	twice
A. deliciosa var. *chlorocarpa*	imperfect to well-developed	mostly pentagonal occasionally quadrangular	0.3-1 mm, medium	twice

Footnote: * numbers are different genotypes

TABLE 2.9 LEAF VENATION AND MARGINS OF SOME *ACTINIDIA*

Taxon	margin types (*) = abaxial tooth hair	marginal teeth orientation	teeth size (mm)
A. arguta var. *arguta*	serrulate teeth compound	45° ascending protuberant	1.00 – 2.00
A. arguta var. *cordifolia*	serrulate teeth compound	45° outwards protuberant to ascending	0.50 – 1.00
A. rufa	serrulate teeth compound	<45° ascending appressed	1.00 – 2.00
A. melanandra var. *melanandra*	serrulate, shallow teeth compound	<45° ascending appressed to downward	0.25 – 0.50
A. kolomikta	serrulate teeth compound	45° ascending to outwards	2.00 – 10.00
A. polygama	serrulate teeth compound	<45° ascending to outward appressed smaller teeth	0.50 – 1.00
A. valvata	serrulate teeth compound	<45° ascending appressed	0.50 – 1.00
A. callosa var. *henryi*	serrulate teeth compound	45° outwards protuberant to ascending	1.00 – 2.00
A. chrysantha	serrulate to crenulate teeth compound	<45° ascending appressed	0.50 – 1.00
A. indochinensis	crenulate upper 1/3 to 2/3 of margin base entire	<45° ascending appressed	0.50 – 1.00
A. melliana	undulate, sinuous teeth compound	<45° ascending appressed	1.00 – 2.00
A. hemsleyana var. *hemsleyana*	serrulate to crenulate teeth compound	45° outwards and appressed protuberant to ascending	0.50 – 1.00
A. latifolia	crenulate, sinuous teeth compound	45° ascending appressed	0.50 – 1.00
A. eriantha	ciliate, denticulate (*) teeth compound	90° outwards protuberant	1.00 – 2.00
A. chinensis var. *chinensis* 3/6/14 b**	repandate, ciliate (*) teeth compound	90° outwards protuberant	1.00 – 2.00
A. chinensis var. *chinensis* 460/4 **	slightly repandate, ciliate (*) teeth compound	90° outwards protuberant	1.00 – 2.00
A. chinensis var. *chinensis* 460/9 **	strongly repandate , ciliate (*) teeth compound	90° outwards protuberant	1.00 – 2.00
A. deliciosa var. *deliciosa* 'Bruno'	crenulate (*) teeth compound	90° outwards protuberant	1.00 – 2.00
A. deliciosa var. *deliciosa* 'Hayward'	crenulate, sinuous near base (*) teeth compound	90° outwards protuberant	1.00 – 2.00
A. deliciosa var. *deliciosa* 'Matua'	denticulate to crenulate (*) teeth compound	90° outwards protuberant	1.00 – 2.00
A. deliciosa var. *chlorocarpa*	ciliate, pectinate (*) teeth compound	90° outwards protuberant	1.00 – 2.00 2.00 – 3.00

Footnote : ** numbers are different genotypes

TABLE 2.9 (continued)

Taxon	margin orientation	course of principal veins in marginal teeth	colours of marginal teeth
A. arguta var. *arguta*	revolute	eccentric	light green yellow-brown tip
A. arguta var. *cordifolia*	revolute	eccentric	light green slight red-brown tip
A. rufa	slightly revolute	eccentric	light green red-brown tip
A. melanandra var. *melanandra*	slightly revolute	eccentric	green orange-brown tip
A. kolomikta	slightly revolute	eccentric	red-brown to purple pink-brown tip
A. polygama	slightly revolute	direct to eccentric	yellow-green red-brown tip
A. valvata	markedly revolute	direct to eccentric	yellow-green yellow-ochre tip
A. callosa var. *henryi*	virtually planar	eccentric	yellow ochre red-brown to purple tip
A. chrysantha	revolute	centric	yellow-green red-brown to purple tip
A. indochinensis	revolute	centric	yellow-green to ochre brown tip
A. melliana	markedly revolute	eccentric	brown to red purple entire tooth
A. hemsleyana var. *hemsleyana*	markedly revolute	centric	yellow-green orange-brown tip
A. latifolia	revolute	eccentric	mid-green red-brown tip
A. eriantha	slightly revolute mostly planar	eccentric	green red-brown tip
A. chinensis var. *chinensis* 3/6/146*	planar	centric	green to brown tooth red-brown to purple tip
A. chinensis var. *chinensis* 460/4*	planar	centric	teeth red-brown to purple
A. chinensis var. *chinensis* 460/9*	planar	centric	teeth red-brown to purple
A. deliciosa var. *deliciosa* 'Bruno'	planar	centric	green to brown red-brown to purple tip
A. deliciosa var. *deliciosa* 'Hayward'	planar	centric	green to brown red-brown tip
A. deliciosa var. *deliciosa* 'Matua'	planar	centric	green tooth purple-brown tip tomentose near base
A. deliciosa var. *chlorocarpa*	planar	centric	long green tooth with purple-brown tip

Footnote: * numbers are different genotypes

2.3.2.8 *Leaf venation and margins*

Margins of *Actinidia* leaves (Table 2.9) all have alternating long and short (compound) teeth, which are supplied by secondary and tertiary veins, respectively. The teeth of most *Actinidia* have distinctive red-brown to purple pigmentation. Teeth can be diminutive or intermediary in form to recognised types of margins (Radford *et. al.* 1974) in many *Actinidia.* Most *Leiocarpae* have leaves with serrulate margins, whereas *Stellatae* usually show variations of the crenulate form. Margins of *Maculatae* and *Strigosae* are intermediary in form between leaves of the former sections. Teeth are typically glabrate, but for the ciliate, tomentose margins of the *Stellatae* e.g. *A. deliciosa* var. *chlorocarpa.*

The orientation of the marginal teeth is apparently related to the planation of the margin. Downwardly curved (revolute) margins are usually associated with marginal teeth whose sinus angles are narrow (10-20°), so that these teeth appear to ascend toward the apex. The protuberant teeth of the *Stellatae* emerge at 90° angles from planar margins. Outwardly pointing teeth are invariably supplied by centrally positioned ("centric") principal veins (Figure 2.14), in contrast to the parietally located ("eccentric") principal veins of ascending teeth (Figure 2.2B).

Some taxa have peculiar margin types such as the undulate, to sinuous ("wavy") margins in *A. melliana* and the widely-spaced and irregularly crenulate or repandate margins of *A. chinensis (*see also Planchon 1847).

Marginal teeth are generally not distinctive along their uppermost surfaces except for those of *A. valvata* (Figure 2.3), *A. arguta* var. *cordifolia* in which the principal vein of the tooth appears as a swollen "glandular pad" of tissue (see Hickey 1979, page 38). Teeth are usually hyaline and glabrescent in their apical regions, but their basal regions may be tomentose abaxially, e.g. *A. eriantha, A. chinensis; A. deliciosa* (Table 2.9).

2.3.2.9 *Marginal hydathodes in Actinidia leaves*

The pronounced development of "glandular teeth" (Hickey 1979) occurring as extensions of veins on the margins of leaves, (Plate 2.4A,C) particularly in the *Stellatae,* their protuberant orientation (Figure 2.4C) and the densely porate nature of the outer surfaces (Plates 2.4B), suggest that these teeth are marginal hydathodes.

The surfaces of the teeth are covered with stoma-like structures which are smaller than stomata of the lower surface. In addition, the "hydathode-stomata" lack the cuticular striations and are smaller and flatter in profile than stomata on the abaxial surface. *Actinidia* leaves are hypostomous, in that stomata are absent from the adaxial (upper) surface of the leaf.

Recognition of "hydathodes" in *Actinidia* is confirmed by studies of their internal organisation and through observations of water excretion in the field. Guttation (= water exudation) is most evident immediately after rainfall and in newly opening leaves early in spring. Guttation has only been observed early in the morning. Unlike other secretory structures (Fahn 1979), hydathodes cannot be identified on the basis of a chemically distinctive product, e.g. rubber, oil or sugar solutions.

2.3.2.9.1 *Histology of hydathodes*

The histological structure of hydathodes (Plate 2.4D) in *A. deliciosa* becomes more diffuse with proximity to the tip and the centre (core) of the gland. Structural specialisation is most obvious at the tip of the hydathode, near the termination of the principal vein.

The base of the gland is compact in structure without exaggeration of the intercellular spaces, like stem or leaf cortical tissues. The structural transition from the lamina to the hydathode is abrupt.

The "distal zone" of the hydathode is delimited by a sheathing layer of mucilaginous, raphide cells which immediately surround the major vascular bundle of the principal vein. Centripetal to the vein is a "secretory zone" composed of irregularly convoluted to amoeboid-shaped parenchyma cells, which form an inner field of "secretory epithem" tissue. Cells of the epithem have thin walls and densely staining contents. Tracheids of the finest diameter end blindly in the smallest parenchyma cells of the epithem. The intercellular spaces of the epithem are large and these are often abutted by the distal[2] walls of tracheids (Plates 2.4D, 2.5B). The "intercellular continuum" enlarges subepidermally toward the substomatal chamber. Elsewhere for a depth of two to three cells below the epidermis, the cells are isodiametric and cortical in appearance with a closely packed arrangement of square to cylindrical cells.

2.3.2.9.2 *Electron microscopy of hydathodes*

Most outermost epidermal and "cortical" cells (Plate 2.5B) are not obviously differentiated and like many mature cells they consist of a large central vacuole, which is surrounded by a "sleeve" of parietal protoplasm. The outer cytoplasm has a reasonably active complement of mitochondria, G.E.R.L.[3] and vesicular

[2]Distal is used with reference to the leaf margin.

[3]GERL is an acronym for Golgi-Endoplasmic Reticulum used by Marty (1978)

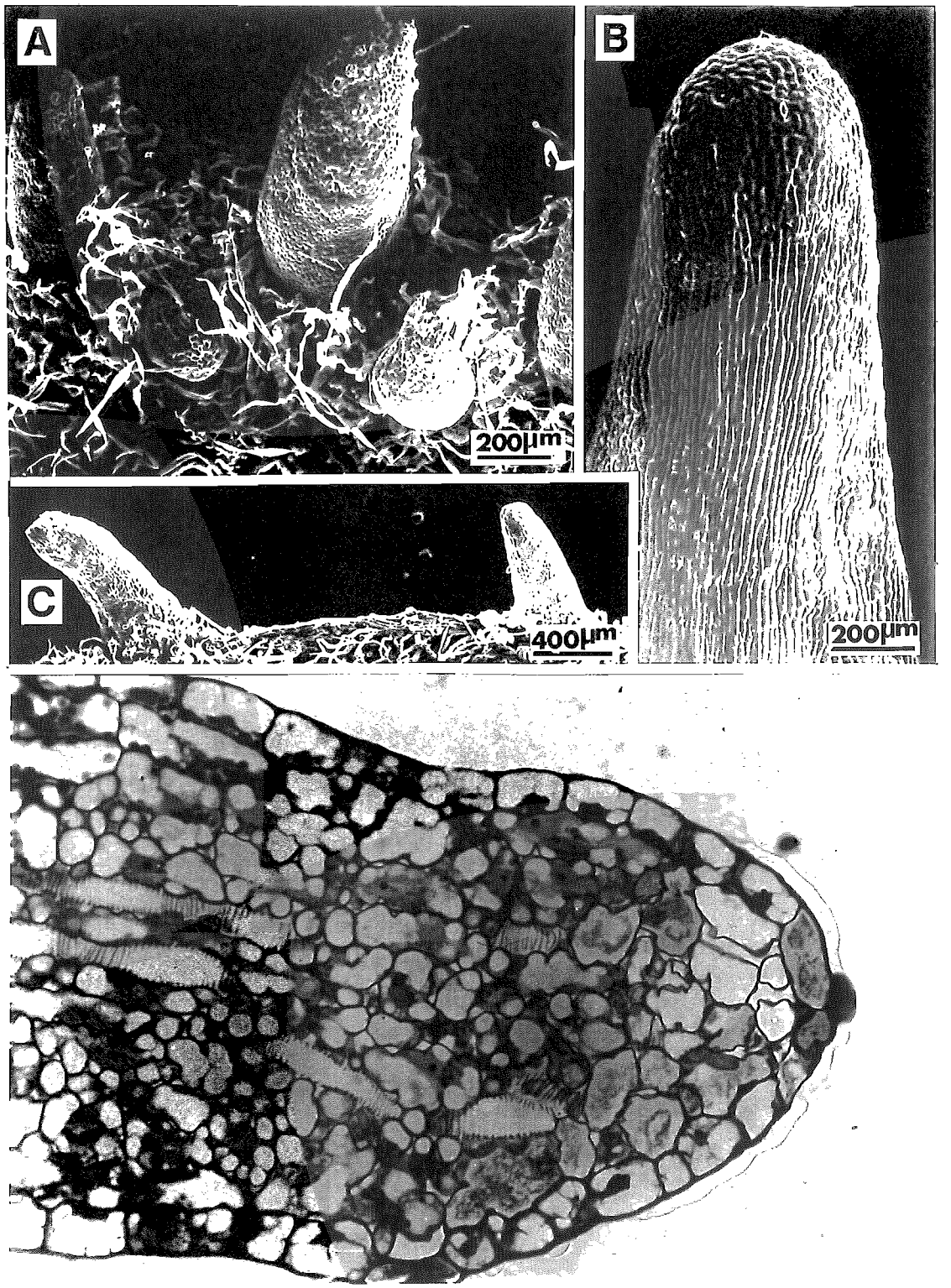


PLATE 2.4 Hydathode morphology.

A Juvenile leaf of *A. chinensis* var. *chinensis*.
B Mature hydathode in *A. melanandra* with stomata open.
C Young leaf margin *A. deliciosa* var. *chlorocarpa* (2 hydathodes).
D L.S. hydathode in *A. deliciosa* var. *deliciosa* cv. Hayward.

endomembranes, particularly near the plasmalemma (Plate 2.5A). Chloroplasts in these cells are diminutive and thylakoids are generally rudimentary in structure, although the hydathodes are obviously "green" in appearance when observed with the naked eye vacuoles are filled with a dispersed reticulum of unknown composition. Cell walls in this region are noticeably thickened, especially in the corners of epidermal cells.

Cells of the secretory epithem are immediately obvious by their amoeboid form, which paradoxically maximises intercellular contacts and intercellular spaces (Plate 2.5B). Vacuoles are proportionately huge and the primary walls of these cells are extremely thin. The ultrastructural complexity of these cells is enhanced near the tracheids, where mitochondrial density, chloroplast development and golgi activity are most pronounced (Plate 2.5E). The plasmalemma is often associated with endomembranes such as GERL vesicles, plasmatubules and multivesicular aggregations. Nuclei are extensively convoluted and the nuclear envelope is traversed by high numbers of nuclear pores (Plate 2.5C).

Tracheary elements (T.Es) comprising the ultimate veins are empty at maturity (Plate 2.5B). The primary walls of these elements are extremely thin and these have widely spaced thickenings of secondary wall material. The youngest T.E's seen are packed with golgi vesicles, E.R. membranes and mitochondria with high numbers of swollen cristae. The primary wall is thickest where the "crossbars" attach, but elsewhere the arrangement of the microfibrils is diffuse, particularly nearest the "freespace-continuum" (Plate 2.5B).

Raphide cells are cytologically complex even at maturity (Plate 2.5C). The parietal cytoplasm has many tubular vacuoles, golgi aggregations and mitochondria with granular matrices. The parietal protoplasm delimits a large vacuole, which is filled with dispersed reticulate material, together with "hard-edged" structures - the remains of raphides (Clark, Smith and Walker 1987). The crystals appear as "hard-edged" silhouettes in thin sections, as their matrices dissolve during processing for T.E.M. The raphides are perfectly intact after freeze-fracturing and freeze-drying for S.E.M. by the method of Fineran and Condon (1988). The raphides are surrounded by contents which are histochemically demonstrable with P.A.S-staining (Feder and O'Brien 1968).

PLATE 2.5:

A Epidermal cells of hydathode showing transition from "cuticle proper" to reticulate region near primary wall-middle lamella. Protoplasm is rich in E.R. and mitochondria.

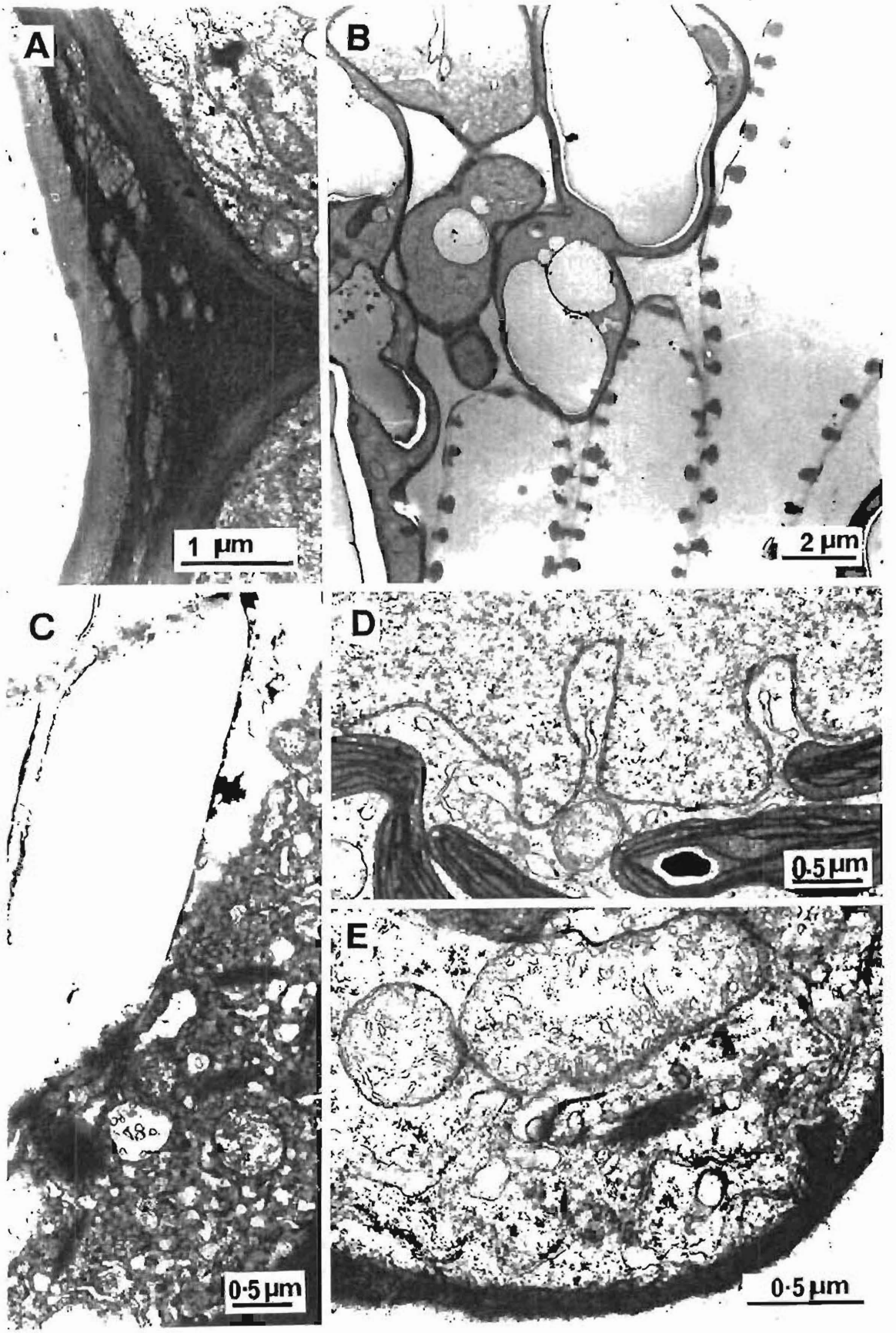
B Junction of tracheid termini with amoeboid-like epithelial cells. Thin primary walls of tracheids abut open spaces of intercellular region.

C Young raphide cell with silhouettes of calcium oxalate crystals within the vacuole and parietal cytoplasm rich in G.E.R.L. endomembranes (including dictyosomes, vesicles and cisternae), tubular vacuoles and mitochondria.

D Nucleoplasmic invaginations of secretory epithelial cell. Nuclear pores are conspicuous as are mitochondria and chloroplasts. E.R. profiles are near the outer nuclear envelope.

E Overview of metabolically active environment of secretory epithelial cell. Mitochondria are well-developed as are G.E.R.L. endomembranes. Rough E.R. is common. Dense lomasomal vesicular aggregation near wall reminiscent of wall process.

(A-E of hydathode *in A. deliciosa* cv. Hayward).


A
1 µm
B
2 µm
C
0·5 µm
D
0·5 µm
E
0·5 µm

2.3.3 Surfaces of mature leaves

Leaf surfaces form an important source of immediately accessible taxonomic characters. The application of scanning electron microscopy to taxonomic studies has almost become routine (Heywood 1971 and has even revealed differences at the infraspecific (cultivar) level (Krause 1978, 1982; White 1986a).

2.3.3.1 *Adaxial (uppermost) surface*

The adaxial surfaces of most *Actinidia* leaves (Table 2.10) are semi-glossy or matt in appearance, but, leaves of *A. rufa (Leiocarpae)* and those *Maculatae* studied have distinctly lustrous surfaces.

Most plants have leaves of "dark" to "mid-green" colouration with the *Leiocarpae* having generally darker leaves than most other *Actinidia.* Members of the *Leiocarpae*, series *Solidae* have green foliage with prominent areas of silver to white variegation, which may exceed half the lamina area in coverage.

The upper surfaces of leaves are completely hairless (glabrous), or sparingly (glabrate) or fully covered (pubescent) with hairs (also termed trichomes, tomentum or indument). Where hairs are diminutive and are represented only by the remains of stubble or hair bases (see Chapter Three also), the surfaces are termed puberulous.

Adaxial surfaces of *Leiocarpae* leaves are mainly glabrate, but for scattered bristle-like (setose) hairs near the margins, or on parietal secondary veins.

Hair qualities are more difficult to define, but here I mainly follow the guidelines in Radford *et. al.* (1974).

Strigose	=	short hairs with swollen bulbous bases
Setose	=	longer, thicker hairs whose shape tapers gradually toward the tip. Form of hair is somewhat bristle-like.
Hirsute	=	very long, stiff hairs straight or curved in their course, e.g. *A. melliana.*
Hispid	=	short to medium length "stiff" hairs not obviously bulbous toward the base, (e.g. stems of *A. deliciosa*).

(Hair dimensions for some *Actinidia* are given in Table 2.13).

Application of these terms is not always easy (see also Stace 1965).

Leaves of *Maculatae* and *Strigosae* have strigose or setose hairs of red to purple colouration which are most evident on the bases of primary and secondary

veins of the adaxial surface. *Stellatae* have the most pubescent leaves, with a cover of fine white hairs or hair bases particularly on basipetal regions of primary and secondary veins. *A. deliciosa* var. *chlorocarpa* is distinguished by a widespread cover of stiff (hispid) orange-brown hairs over most of the adaxial surface of the lamina.

2.3.3.2 *Abaxial (lowermost) surface*

The abaxial surfaces of *Actinidia* leaves (Tables 2.11, 2.12) are more complex in structure and provide more characters than the adaxial surfaces. Subdivision of the genus into sections is based upon the type and abundance of hairs on the abaxial leaf surface (Li 1952).

The lower surfaces of most leaves have a glaucous (blue-green) or white caste (Table 2.11). The apparent colour of the leaf is the result of light reflecting from all surface structures. The brown caste of *A. deliciosa* leaves derives from the different colours of various orders of venation and the overlying hairs (Table 2.12). The textural coarseness and reflectivity are apparently related to epidermal papillation (Plate 2.8A) and convexity of the outermost walls (Plate 2.8E). A "scaly" or lepidote texture is associated with the incidence of epicuticular waxes (Plate 2.8A). Cuticular striations associated with stomata (Plate 2.8E) may also cause the underside of the leaf to glisten.

The abundance of abaxial hairs increases from the *Leiocarpae* to the *Stellatae* as described by Dunn (1911), Li (1952) and Liang (1984).

Leiocarpae (except *A. rufa*) have simple, strigose hairs in the axils of secondary veins, which appear as tufted or beard-like structures (see Liang 1984). Trichomes are common along the sides of veins in *A. kolomikta*, but not in leaves of other *Leiocarpae*.

Anomalous hair types, not described elsewhere, occur in *A. arguta* var. *cordifolia* and *A. rufa*, presently placed in the *Leiocarpae* (Liang 1984).

In *A. arguta* var. *cordifolia* simple, "spiny", setose hairs develop as secondary structures on basipetal regions of primary and secondary veins in mature leaves. These structures are initiated long after abscission of the juvenile indument formerly clothing the surfaces of younger leaves.

Axillary hairs near the primary vein of *A. rufa* are frequently stellate and branch near the surface of the leaf. They differ from hairs of most *Stellatae*, in that they are not stalked, nor do they branch from pedicellate bases.

The hair complements of leaves from sections *Maculatae* and *Strigosae* are also diverse.

Table 2.10 Adaxial leaf surface characters in mature leaves of *Actinidia*

Taxon	Mature leaves gloss	colour	Hairs present/absent hair location
A. arguta var. *arguta*	semi-glossy	dark green	glabrate red-brown hairs[2] near margins
A. arguta var.*cordifolia*	semi-glossy	dark green	glabrate red-brown hairs[2] near margins
A. rufa	glossy	dark green	puberulous red-brown hair bases[1] on bases of 1°,2° veins
A. melanandra var. *melanandra*	matt	mid-green	glabrous
A. kolomikta	glossy	dark olive green	puberulous red-brown hairs[2] at junctions of most veins, rare on 2° except near margins
A. polygama	matt	variegated white and green	glabrate[1] near margins on parietal 2° veins, hairs[1] glassy, but red speckled at "joints", rarely[2]
A. valvata	matt	variegated yellow-green, silver-white	glabrate[2] near margins on parietal 2° veins, hair glassy
A. callosa var. *henryi*	glossy	dark green	glabrate red-brown hairs[1] on base of 1° vein and petiole
A. chrysantha	glossy	mid to dark green	veins near base puberulous orange-red hair[1] bases
A. indochinensis	glossy	mid to dark green	glabrous
A. melliana	glossy	mid to dark green	glabrate red-purple hairs[2] 1°, 2° veins red hair[1] bases
A. hemsleyana var. *hemsleyana*	semi-glossy	mid-green	puberulous glassy red hair[1] bases, hairs[1,2] common near margin

Continued .....

Table 2.10 continued....

Taxon	Mature leaves gloss	colour	Hairs present/absent hair location
A. latifolia	glossy	mid-green	glabrate hairs[1] white to glassy on vei
A. eriantha	semi-glossy	light to grass-green	pubescent fine white to glassy hairs[1,2] not esp. dense
A. chinensis var. *chinensis* 3/6/14b*	semi-glossy	dark green	pubescent esp. when young white hairs[2] on most veins esp.1°
A. chinensis var. *chinensis* 460.4*	semi-glossy	dark green	puberulous white hairs[2] on most veins esp 1°
A. chinensis var. *chinensis* 460.9*	semi-glossy	dark green	puberulous white hairs[2] on most veins esp 1°
A. deliciosa var. *deliciosa* 'Hayward'	glossy	bright, olive-green	sparingly pubescent red-brown hairs[1] sides of 1°, 2° veins
A. deliciosa var. *deliciosa* 'Matua'	glossy	mid-green	puberulous red-brown hair[1] bases 1°, 2° veins
A. deliciosa var. *deliciosa* 'Bruno'	semi-glossy to matt	mid to dark green	pubescent 1°, 2° veins with white hairs these veins black near base
A. deliciosa var. *chlorocarpa*	semi-glossy to matt	mid to light green	pubescent, hispid orange-red hairs[1] widesprea esp. on veins

Footnotes : Superscripts = hair types (source Radford *et al.* 1974)
1 = simple strigose
2 = simple setose
3 = stellate
4 = setose "spiny" "2° hairs"
5 = hirsute (simple)
6 = red-brown droplets = remains of hair bases adhering to surface
* Numbers are different genotypes.

Abbreviations:
esp = especially,
occ = occasionally,
ns = non-stalked
1° = primary
2° = secondary

Table 2.11(a) **Abaxial leaf surface characters in mature leaves of some *Actinidia***

Taxon	Colour of surface	Hair abundance
A. arguta var. *arguta*	white to light green	bearded axils of 2°
A. arguta var.*cordifolia*	Light green to white	bearded axils of 2°
A. rufa	white to green	bearded axils of 2°s
A. melanandra var. *melanandra*	blue-green	bearded axils of 2°
A. kolomikta	olive green	bearded axils of 2°
A. polygama	blue-green	puberulous on veins
A. valvata	blue-green	glabrate
A. callosa var. *henryi*	olive-green	bearded axils of 2°
A. chrysantha	blue-green	glabrate
A. indochinensis	blue-green to white	glabrate
A. melliana	blue-green, pruinose glaucous	puberulous
A. hemsleyana var. *hemsleyana*	blue-green	puberulous minutely downy
A. latifolia	blue-green	tomentose
A. eriantha	blue-green	tomentose
A. chinensis var. *chinensis* 3/6/14b*	white-to green	tomentose
A. chinensis var. *chinensis* 460.4*	white to green	tomentose
A. chinensis var. *chinensis* 460.9*	white to green	tomentose
A. deliciosa var. *deliciosa* 'Hayward'	pale green	tomentose
A. deliciosa var. *deliciosa* 'Matua'	blue-green	tomentose
A. deliciosa var. *deliciosa* 'Bruno'	blue-green with ochre hue	tomentose
A. deliciosa var. *chlorocarpa*	blue-green with green hue	tomentose

Continued....

Footnotes : * Numbers are different genotypes.

Table 2.11(b) Abaxial leaf surface characters in mature leaves in some *Actinidia*

	Hair type and distribution	Interveinal texture (+ stereo L.M.)
A. arguta var. *arguta*	1°,2° vein axillary hair[2] tufts hairs, white with red-brown tips	finely felt-like to scaly (lepidote)
A. arguta var.*cordifolia*	1° vein pale red hairs[1,4] 2° vein axillary hairs[1]	finely felt-like
A. rufa	1°,2° vein axillary red-brown hair tufts[1,3] (3=n.s.)	finely felt-like
A. melanandra var. *melanandra*	1°2° vein axillary glassy, red-brown speckled hair tufts[1]	soft to felt-like
A. kolomikta	1° to 4° veins red-speckled glassy hairs[1,2] mostly in sides; 1°,2° vein small axillary hair tufts[1],white	finely felt-like, glistening
A. polygama	1° vein with glassy pale red-specked hairs[1] occ[2] 2° vein axillary hair tufts[1]	felt-like, glistening
A. valvata	1° vein with glassy pale red-speckled hairs[1]occ[2] 2° vein axillary hair tufts[1] occ. on 3° veins	finely felt-like glistening
A. callosa var. *henryi*	1°,2° veins red hair tufts[1,3] (3=n.s.) on sides and axils	finely felt-like,
A. chrysantha	1°,2° sporadic red hairs[1] and sporadic interveinal hair bases[6]	finely felt-like, glistening overlain by coarse wax flakes
A. indochinensis	1°,2° veins orange brown hairs[1] on sides and hair bases[6] interveinally	minute scales,lepidote
A. melliana	1°,2°,3° veins red-purple hairs[2,5] on sides esp.1°	felt-like to finely lepidote
A. hemsleyana var. *hemsleyana*	1°,2°,3° veins with sparce cover of fine white[1,2],and fine red-brown hairs[2] = bifids	finely felt-like, glistening
A. latifolia	1°,2° veins red-brown hairs[1] on upper surface (3=n.s) white hairs[3] on sides,elsewhere mostly[3]	coarsely felt-like

Continued....

Table 2.11(b) Cont....

	Hair type and distribution	Interveinal textu (+ stereo L.M
A. eriantha	incanescent pubescent[1,3] dense (3=n.s)	woolly incanescer
A. chinensis var. *chinensis* 3/6/14b*	1°,2° veins whitish to glassy hairs[1] on tops,white hairs[1,3] elsewhere mostly[3]	felt-like, glistenin
A. chinensis var. *chinensis* 460.4*	1°,2° veins whitish to glassy hairs[1] on tops,white hairs[1,3] elsewhere mostly[3]	felt-like, glistenin
A. chinensis var. *chinensis* 460.9*	1°,2° vein ochre-brown hairs[2] on tops, white hairs [2,3] elsewhere, mostly[3]	felt-like, glistenin
A. deliciosa var. *deliciosa* 'Hayward'	1°,2° vein, red-brown hairs[1] on tops, white hairs[1,3] elsewhere, mostly[3]	felt-like, glistenin
A. deliciosa var. *deliciosa* 'Matua'	1°,2° vein red-brown hairs[1] on tops, white hairs[1,3], elsewhere mostly[3]	felt-like, glistenin
A. deliciosa var. *deliciosa* 'Bruno'	1°,2° vein red-brown hairs[1] on tops, white hairs[1,3], elsewhere, mostly[3]	felt-like, glistenin
A. deliciosa var. *chlorocarpa*	1°,2° veins red-ochre hairs[2] on tops white hairs[1,3], elsewhere mostly[3]	finely felt-like, glistening

Footnotes : Superscripts = hair types (sources Radford *et al.* 1974, Payne 1978)
1 = simple strigose
2 = simple setose
3 = stellate
4 = setose "spiny" "2° hairs"
5 = hirsute (simple)
6 = red-brown droplets = remains of hair bases adhering to surface
* Numbers are different genotypes.

Abbreviations: esp = especially,
occ = occasionally,
ns = non-stalked
1° = primary
2° = secondary

Table 2.12 Abaxial surfaces of outer leaves in *A.deliciosa* and some related taxa

Taxon	No. of branches per stellate hair; hair density[1] (mm^{-2})	Overall abaxial colour	1° vein thickness[2] 2° vein relative size[2]	1° 2° colour of vein colour of hairs colour of hair base	3°; Higher Venation colour of vein colour of areolation hair base colour
A. chinensis var. *chinensis* 3/6/14b*	7-8 8.00 ± 0.14	greyish blue-green with brown hue	weak moderate to fine and hair-like	-veins chocolate brown -hair whitish glistening -hair base pale pink to ochre	-veins green flecked with red purple -areoles dark-brown to red-purple -hair base almost colourless pale pink to ochre
A. chinensis var. *chinensis* 460.4*	8-10 9.80 ± 0.20	greyish blue-green with brown hue	weak moderate to fine and hair-like	-veins chestnut brown to dark brown-hairs whitish glistening -hair base pale pink to ochre	-3°'s greenish red-purple -areoles red-purple to black -hairbase pale pink to ochre
A. chinensis var. *chinensis* 460.9*	8-10 9.20 ± 0.16	greyish blue-green green with ochre hue	weak moderate	-veins pale chestnut -hairs pale yellow to white -hair bases pale orange to brown	-3°,4° pale ochreish green -areoles red-purple to black -hair base pale pink to ochre
A. deliciosa var. *deliciosa* 'Bruno'	6-9 7.60 ± 0.29	ochreish blue-green	stout moderate	-veins yellow to ochre -hairs whitish -hair bases ochre to brown	-3°,4° pale ochreish green -areoles dark to black -pale pink to ochre hair base

Table 2.12 continued .....

Table 2.12 continued.....

Taxon	No. of branches per stellate hair; hair density[1] (mm^{-2})	Overall abaxial colour	1° vein thickness[2] 2° vein relative size[2]	1° 2° colour of vein colour of hair colour of hair base	3°; Higher Venation colour of vein colour of areolation hair base colour
A. deliciosa var.*deliciosa* 'Matua'	9-11 9.80 ± 0.16	greenish blue-green	moderate moderate	-veins chestnut brown -hair yellow ochre -hair base pale pink to ochre	-3°,4° yellow green with purple flecks -areoles red-purple -pale pink to ochre hair base
A. deliciosa var. *deliciosa* 'Hayward'	8 - 12 10.40 ± 0.33	greenish blue-green	moderate moderate	-veins ochre to light chestnut brown -hair base yellow ochre to cream	-3° yellow-green -areoles dense red-purple to black -hair base pink to ochre
A. deliciosa var.*chlorocarpa*	3 - 5 4.20 ± 0.16	greenish blue-green	moderate moderate	-veins dark chestnut brown -hairs yellow to white setose amd strigose -hair base pale pink to ochre	-3° chestnut-brown to red-purple -areoles red-purple to black -hair base pink to ochre

1. n = 3 sun leaves, 5 areas sampled per leaf
2. criteria after Dilcher 1974
* Numbers are different genotypes

Table 2.13 Hair dimensions of some *Actinidia*

Taxon	Adaxial (μm)	Abaxial (simple) non-branched (μm)	Abaxial branched (μm)
A. arguta var. *arguta*	N.A.		N.A.
A. arguta var.*cordifolia*	N.A.		N.A.
A. rufa			
A. melanandra var. *melanandra*			N.A.
A. kolomikta		150 - 200	N.A.
A. polygama	N.A.	188 - 313	N.A.
A. valvata	N.A.		N.A.
A. callosa var. *henryi*			max diam. 300-850 hair arms 120-520
A. chrysantha			N.A.
A. indochinensis			N.A.
A. melliana			N.A.
A. hemsleyana var. *hemsleyana*			max diam. 297- 3555 hair arms 118 - 1837
A. latifolia		140-210	max diam. 280 - 560 hair arms 84 - 280
A. eriantha	291 - 830		max diam. 160 - 450 hair arms 125 - 300
A. chinensis var. *chinensis* 3/6/14b*	105 - 209		max diam. 500 - 625 hair arms 188 - 500
A. chinensis var. *chinensis* 460.4*			
A. chinensis var. *chinensis* 460.9*			
A. deliciosa var. *deliciosa* cv.Hayward			
A. deliciosa var. *deliciosa* cv. Matua			
A. deliciosa var. *deliciosa* cv.Bruno			max diam. 590 - 1172 hair arms 260 - 520
A. deliciosa var. *chlorocarpa*			hair arms 320 - 480

Footnote : * Numbers are different genotypes.

Stellate, stalked (Plate 2.6A) and non-stalked hairs (Plate 2.6B) are seen in *A. callosa* var. *henryi* (Plate 2.6B), and in *A. hemsleyana* (Plate 2.6C), whereas most other plants from these sections have simple hairs of a strigose or setose type. The hairs of *A. melliana* are long and hirsute.

Abaxial trichomes are most consistent in those *Stellatae* observed in this study.

The upper surfaces of abaxial primary and secondary veins (e.g. *A. latifolia*, Plate 2.8C) are covered with simple, strigose hairs of white to brown colouration, which soon abscise with maturity (e.g. *A. deliciosa* cv. Bruno, Plate 2.8D). The sides and axils of these veins are clothed with numerous glassy, stellate hairs, whose branches are borne on pedicellate or "stalked" bases of multicellular construction (Plate 2.7A,C). These stellate hairs extend beyond the major (primary and secondary) veins to cover most of the abaxial surface. The size density and degree of branching shown by these hairs is diagnostic at species (Gao 1988) and cultivar levels (Tables 2.7, 2.8; 2.12). The simple hairs along the primary veins of most *A. deliciosa* cultivars are strigose, but tending toward setose in appearance. In *A. deliciosa* var. *chlorocarpa* the hairs are noticeably setose, particularly those associated with the pectinal veins.

2.3.3.3 *Surfaces of juvenile leaves*

Even *Actinidia* with the most glabrous leaves at maturity have tomentose apical shoots. Apical leaves of *A. arguta* var. *arguta (Leiocarpae)* are densely covered with simple uniseriate (1-rowed) trichomes *ca.* 100 μm in length (Plate 2.8E). Simple hairs soon abscise from all regions of the leaf but the midrib. Elsewhere the lamina is studded with the vestiges of hair bases e.g. *A. melanandra* (Plate 2.8B), which can give the shoots "a powdery" or pulverent appearance. Marginal hydathodes are usually free of hairs, but for their basal regions in some *Stellatae*.

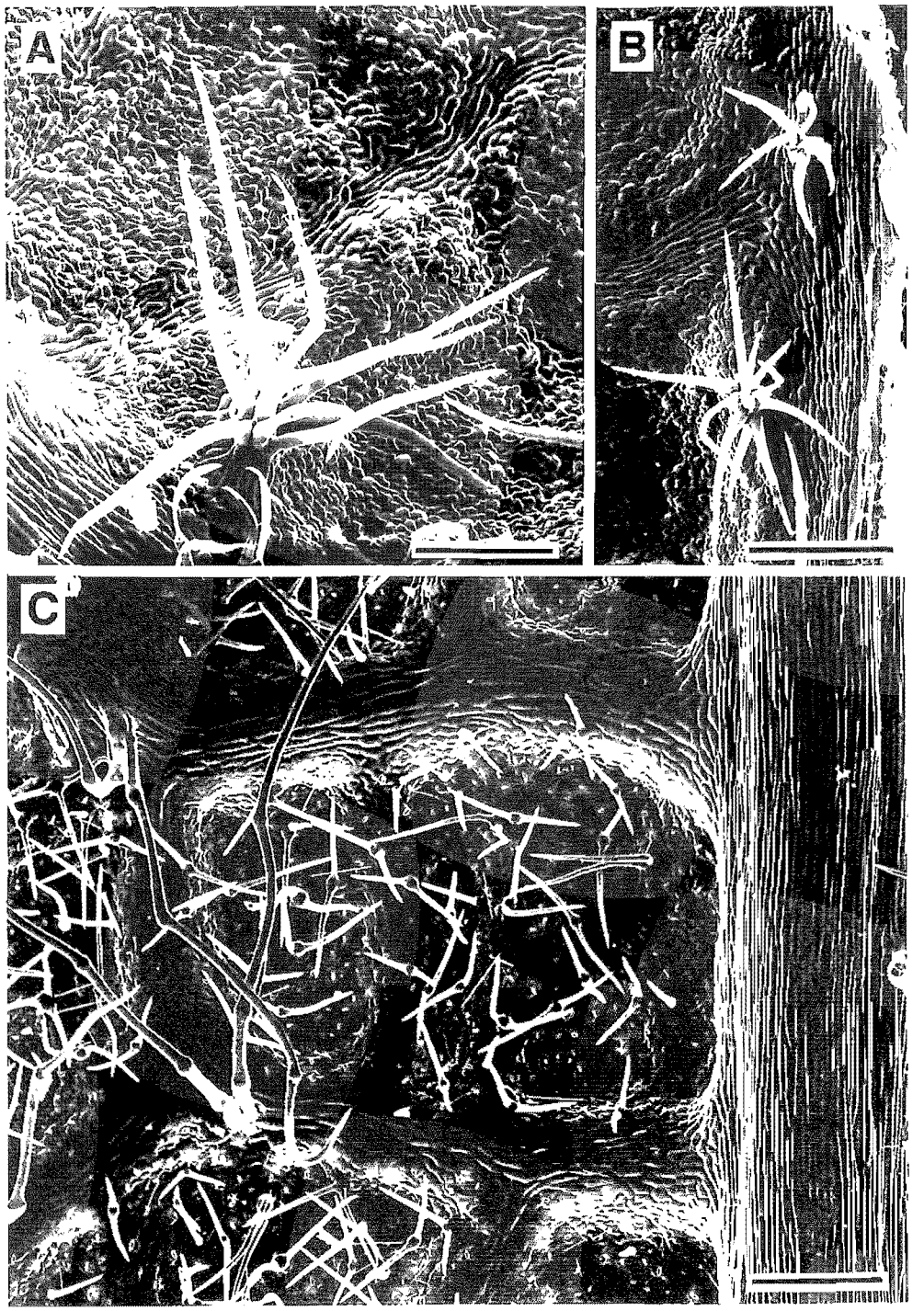


PLATE 2.6:

A; B Stellate leaf hairs on abaxial leaf surface of *A. callosa* var. *henryi* (Maculatae).

C Bifid leaf hairs on abaxial leaf surface of *A. hemsleyana* var. *hemsleyana* (*Strigosae*).

Bar scale = 200 μm

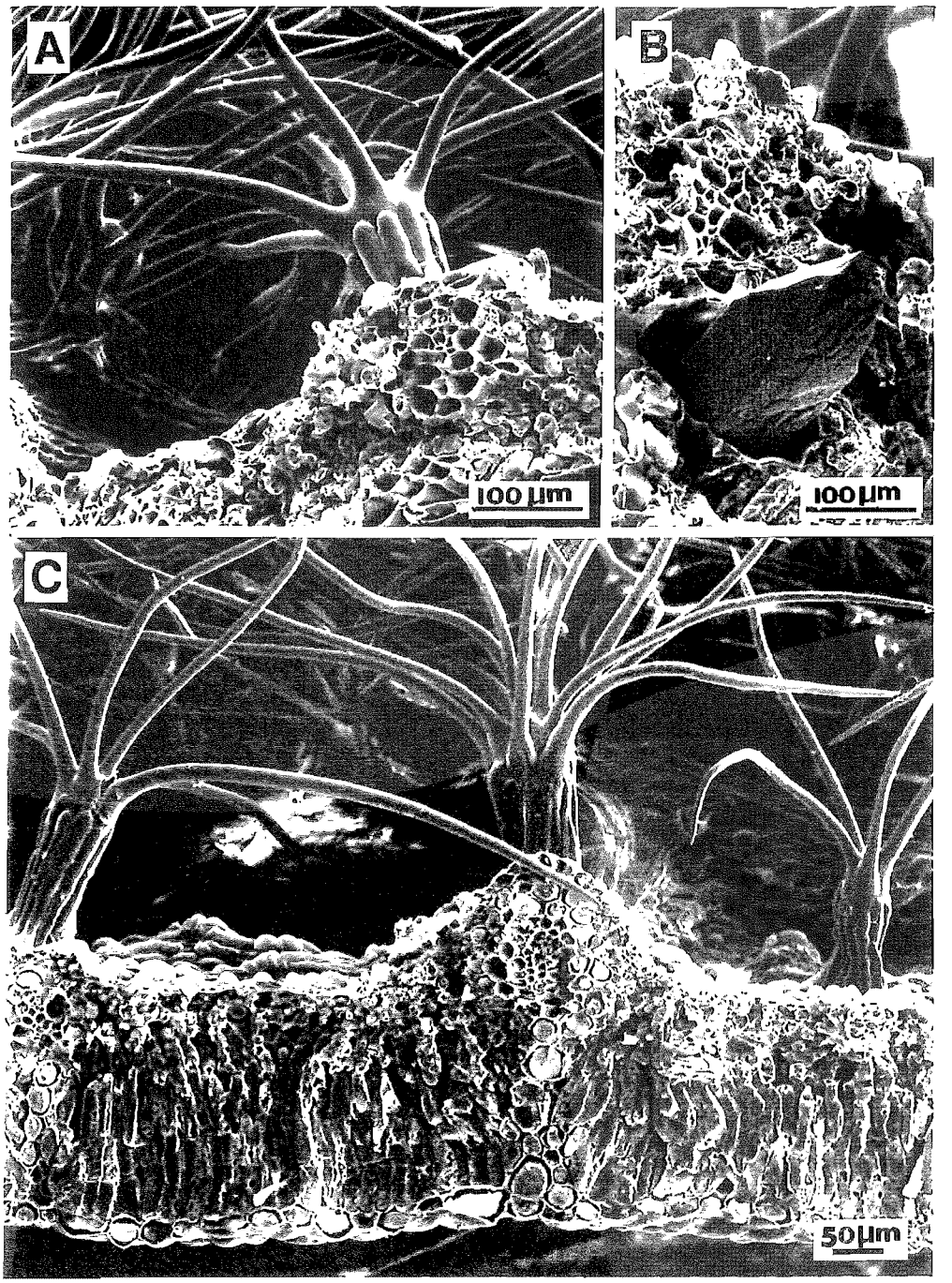


PLATE 2.7:

Abaxial leaf surfaces uppermost, fractures all T.S.

A A leaf of *A. chinensis* var. *chinensis*
B Styloid near bundle of *A. deliciosa* var. *deliciosa* cv. Hayward.
C Stellate hairs near vascular bundles, collenchyma above bundle; high palisade to mesophyll ratio; *A. deliciosa* var. *deliciosa* cv. Hayward.

Bar scale = 100 μm unless stated otherwise

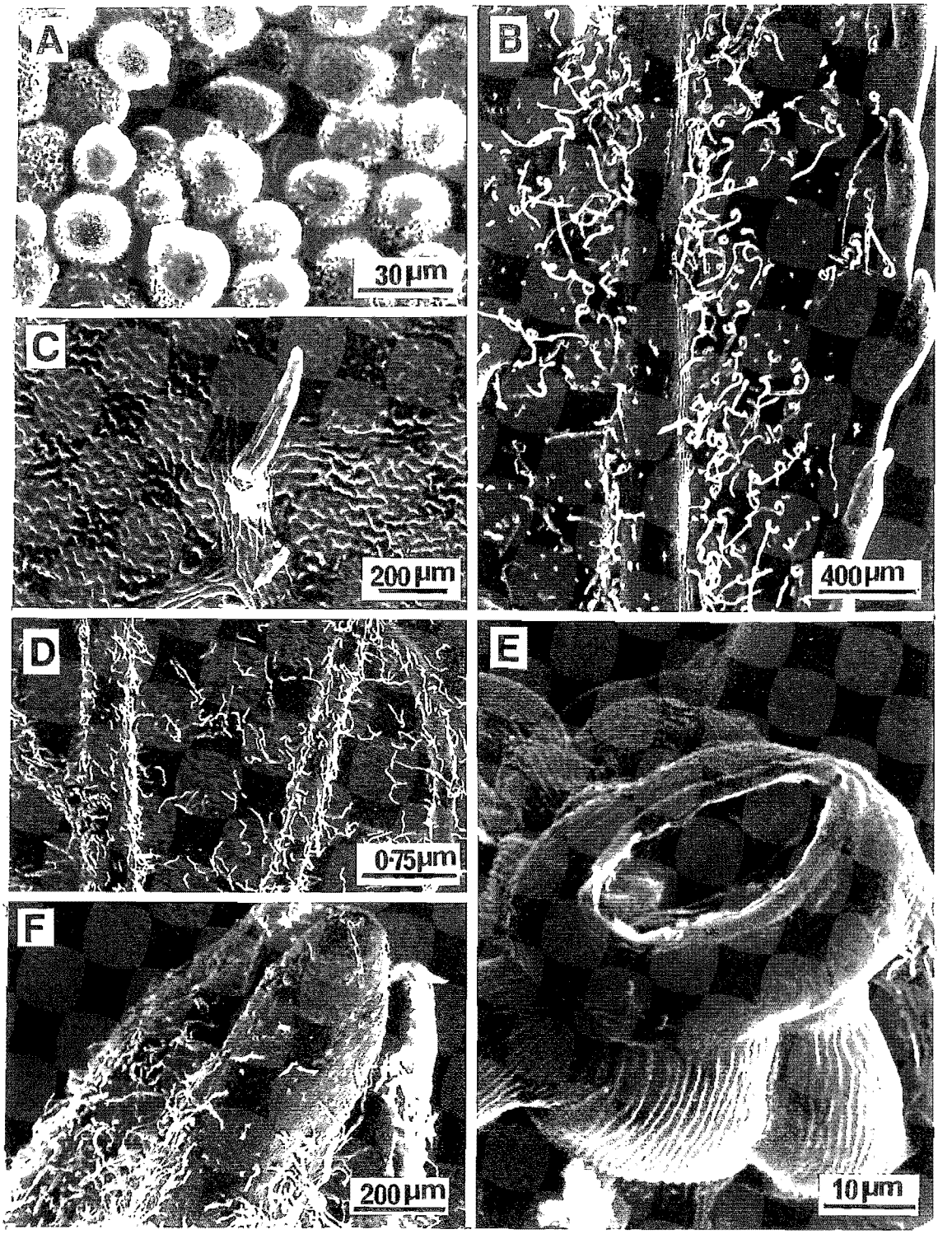


PLATE 2.8:

A Abaxial surface of *A. melliana* leaf, note stoma and epicuticular wax flakes.

B Abaxial surface of *A. melanandra* var. *melanandra* leaf, note simple hairs and marginal hydathodes.

C Adaxial surface of *A. latifolia* simple hairs.

D Abaxial surface, juvenile leaf of *A. deliciosa* var. *deliciosa* cv. Bruno.

E Abaxial surface, stoma of *A. deliciosa* var. deliciosa cv. Hayward.

F Apex of *A. arguta* var. *arguta*, simple caducous hairs.

2.3.4 Anatomy of some *Actinidia* leaves

Despite the anatomical diversity of *Actinidia* leaves (Table 2.15) several features are common at the generic level.

2.3.4.1 *Common trends*

Leaf surfaces are normally described in relation to their orientation within the bud, even once the leaf has expanded fully. The uppermost (adaxial) surface defined as that which faces toward ("ad-") the axis in the bud, is simple in structure. The adaxial cuticle is normal except for its thickness, which always exceeds that of the lower surface. Adaxial epidermal cells are distended in shape, acquiring a convex to inflated appearance in profile.

The interveinal tissues are dorsivenitral in organisation. The leaves have a well-developed mesophyll, which is structurally differentiated into a two-layered palisade parenchyma composed of cylindrical cells which are specialised for light interception; beneath this occurs a zone of spongy mesophyll tissue with variously enlarged intercellular spaces for gas exchange.

The lower epidermis comprises a single layer of inflated convex to papillate cells overlain by a thin cuticle. Stomata project markedly from the abaxial surface. Stomatal size may be taxonomically informative as seen in Table 2.14.

The leaf blade is variously modified among different *Actinidia* to accommodate respective orders of venation (Section 2.3.3). The primary vein is conservative in its anatomical organisation. The adaxial side of the vein is delimited by a local or circumferential zone of supportive collenchyma of primary origin. Most of the vein consists of cortical parenchyma. In cross-section, the anatomy of the bundles in the primary vein may change, subject to the presence or absence of departing secondary veins. The bundle anatomy of the primary vein is most stable nearest the base of the petiole and this is either arc-shaped or circular in cross-section (Gao 1988 and *Actinidia* in this study). Parenchyma cells proximal to conducting tissues are filled with phenolic substances and mucilaginous raphide cells are conspicuous in the phloem and amongst scattered parenchyma cells. Phenolics are histochemically demonstrable using toluidine blue-acid fuschin staining and mucilage reacts positively to toluidine blue-P.A.S. stains (Feder and O'Brien 1968).

Transverse sections obtained parallel to secondary veins of the leaf reveal conspicuous mucilaginous cells of the bundle sheath, which delimit phenolic cells and tracheary elements. Phenolics are also encountered within the palisade cells of most *Actinidia*, in varying quantities.

Table 2.14 Stomatal sizes of some *Actinidia*

Taxon	Stomatal length (μm)	Stomatal width (μm)	Length/width ratio
A. arguta var. *arguta*			
A. arguta var.*cordifolia*	20 - 40[1]	10 - 20[1]	2 : 1
A. rufa			
A. melanandra var. *melanandra*			
A. kolomikta	10 - 20[1]	5 - 10[1]	2 : 1
A. polygama	10 - 20[1]	5 - 10[1]	2 : 1
A. valvata	20 - 40[1]	10 - 20[1]	2 : 1
A. callosa var. *henryi*	13 - 26[1]	5 - 11[1]	
A. chrysantha			
A. indochinensis	20 - 30[1]	6 - 8[1]	
A. melliana	5 - 6[1]	2 - 3[1]	
A. hemsleyana var. *hemsleyana*			
A. latifolia	10 - 20[1]	5 - 10[1]	2 : 1
A. eriantha			
A.chinensis var. *chinensis* 3/6/14b*			
A. chinensis var. *chinensis* 460.4*			
A. chinensis var. *chinensis* 460.9*			
A. deliciosa var. *deliciosa* cv.Hayward	50 - 60[1]	20 - 30[1]	2 : 1
A. deliciosa var. *deliciosa* cv. Matua			
A. deliciosa var. *deliciosa* cv.Bruno			
A. deliciosa var. *chlorocarpa*			

Footnotes : 1 = Freeze dried tissue
* Numbers are different genotypes

Secondary or tertiary veins of most *Actinidia* distend the abaxial lamina downwards. Conducting tissues of the vein are joined to the lower epidermis by a continuous zone of collenchyma fibres. Raphide cells are positioned above and to the side of the vascular tissues.

2.3.4.2 *Taxonomic sectional trends in leaf anatomy* (Table 2.15)

Leiocarpae are typically devoid of epidermal hairs (e.g. *A. arguta* var. *arguta* Plate 2.9A). They lack an interveinal hypoderm and have bundles with or without extensions composed of adaxial collenchyma. Palisade parenchyma is 1- or 2- layered and normally this extends for 0.25 - 0.50 the thickness of the leaf. The interveinal lamina is 0.1 - 0.3 mm in thickness, becoming distended for 1-3 mm near the primary vein. The horizon of the lamina is level with that of the primary vein. The latter is arc-shaped in cross-section near the base of the petiole. Sclerenchyma fibres may form a 2-layered ring around the primary bundle (Plate 2.9A). Phenolic deposits rarely extend beyond the vascular tissues. Spongy mesophyll is diffuse in type (Radford *et al.* 1974) with well-developed air-spaces and the arm-parenchyma has much elongated arms. Thin acicular raphides 3-6 μm wide x 70-100 μm long are the major ergastic structures associated with the veins, larger crystals of cubic cross-section are rare in this group, e.g. *A. arguta* var. *cordifolia*; Plate 2.9D,E.

The abaxial epidermis is relatively smooth and stomata are not raised obviously above the surface.

The anatomy of *Maculatae* leaves is similar to that of the *Leiocarpae* studied. The interveinal lamina is 0.3 - 0.6 mm in thickness, becoming distended for 1-2 mm near the primary vein. Sclerenchyma fibres are either isolated or occur in 2-4 layered rings around the primary vein. Phenolic cells can be common beyond the primary vein, (e.g. *A. chrysantha* Plate 2.9C; *A. indochinensis*), where their dense contents clearly demarcate the subepidermal collenchyma associated with the primary vein.

Leaves of the *Strigosae* (e.g. *A. melliana*, Plate 2.9B) are anatomically similar to examples from the previous sections of the genus. The horizon of the lamina is located above that of the primary vein. Sclerenchyma fibres are rare and these barely form a single continuous layer around the primary bundle. Phenolics seldom extend beyond the bundle tissues. The airspaces are relatively large and the spongy mesophyll is attenuate or globose in form. Raphides are the only ergastic structure noted and the abaxial epidermis is smooth with non-protuberant stomata.

Stellatae have numerous stellate hairs in cross-section borne on complex multicellular bases. The leaves lack an interveinal hypoderm, except for

A. latifolia, and bundles always have prominent adaxial collenchyma extensions *ca.* 2-4 cells wide (Plate 2.10D). Palisade parenchyma is 2-3 layered with much elongated cells (length : width $\geqslant$ 6:1) and this tissue normally comprises 0.75 of the leaf thickness (Plate 2.10A). The interveinal lamina is 0.1-0.3 mm in thickness, becoming distended for 1-4 mm near the primary vein. The horizon of the lamina is below that of the primary vein; the latter is fully closed and circular to ovoid in cross-section near the base of the petiole. Primary bundles are surrounded by prominent 2-4 layered rings of sclerenchyma fibres. Phenolic deposits seldom extend beyond the tissues of the bundle. Spongy mesophyll tissue is diffuse with well-developed air-spaces and parenchyma cells are extremely globose and not attenuated in form (Plate 2.10B). Ergastic structures include acicular raphides and thicker crystals of cubic cross-section (Plate 2.9 D,E). Styloid crystals (*ca.* 10-20 μm wide x 100-200 μm long) are also peculiar to this group (Plate 2.7B). The abaxial epidermis is markedly papillate and stomata are borne on accessory cells, which are conspicuously raised at 45° angles to the surface of the leaf (Plate 2.8E; 2.10B;C).

PLATE 2.9:

A T.S. of leaf of *A. valvata* with primary vein (far left) to leaf blade (far right). Low palisade to spongy mesophyll ratio and diffuse spongy mesophyll are evident.

B T.S. of primary vein (*A. melliana),* note well-developed collenchyma layer.

C T.S. of *A. chrysantha* leaf with abundant blue-green staining of phenolic contents in cortex, hypoderm and phloem. Conspicuous 3-4 layered sclerenchyma surrounding vascular bundle.

D T.S. of *A. arguta* var. *cordifolia* leaf. Raphide cell with blue-staining mucilage above bundle in T.S. Bundle sectioned in oblique L.S. surrounded by thicker crystals of cubic cross-section.

E Inset of 2.9D: cross-section of cell containing cubic crystals ca. 5 times the diameter of the raphides.

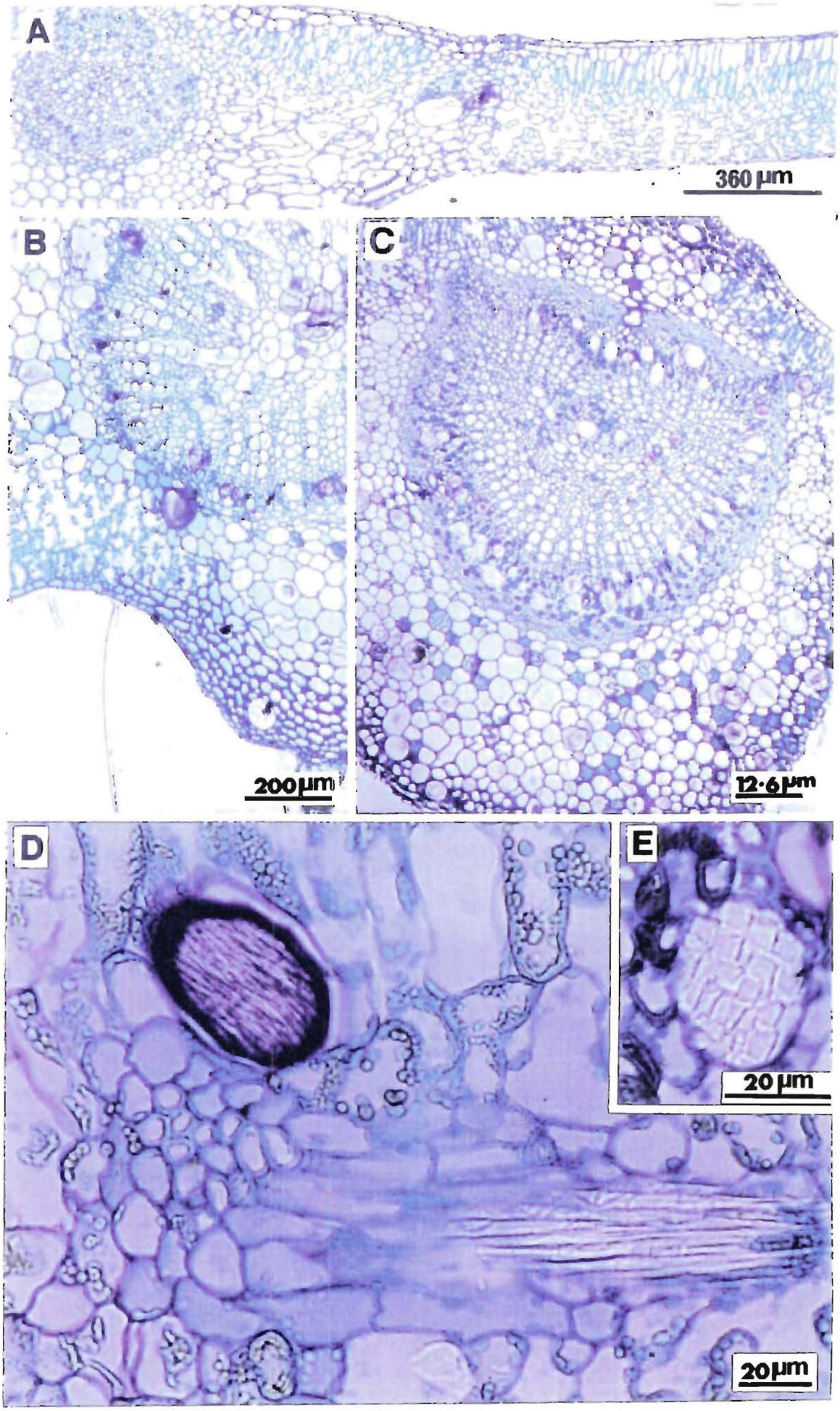

A
360 µm
B
200µm
C
12·6µm
D
E
20 µm
20µm

PLATE 2.10:

A T.S. of leaf in *A. deliciosa* var. *deliciosa* cv. Bruno. Papillate abaxial epidermis with bases of stellate multicellular hairs sectioned below the leaf plane. Collenchyma is conspicuous near veins above the vascular bundles. Styloids appear in L.S. amidst the blue-green palisade cells. Primary vein is large c.f. others; cortex is regular with large empty cells formerly containing crystals.

B Detail of 2.10A. Protuberant stomata borne on raised accessory cells define a conspicuous substomatal chamber, flanked above by globose spongy mesophyll tissue. Leaf is hypostomous; abaxial surface shown.

C Detail of stoma from abaxial surface of *A. latifolia.* Guard cells in medial L.S. plane.

D T.S. of *A. latifolia* leaf with prominent adaxial collenchyma above bundle and tightly packed globose palisade parenchyma to the sides.

E T.S. of an *A. eriantha* leaf with secondary (lateral) bundle on far left and part of the primary bundle (midrib) on the right. Plane of section is just above a vascular bundle running longitudinally between primary and secondary veins, seen in T.S. Bundle tracheids are seen immediately below the line of raphides, which normally encircles the bundle.

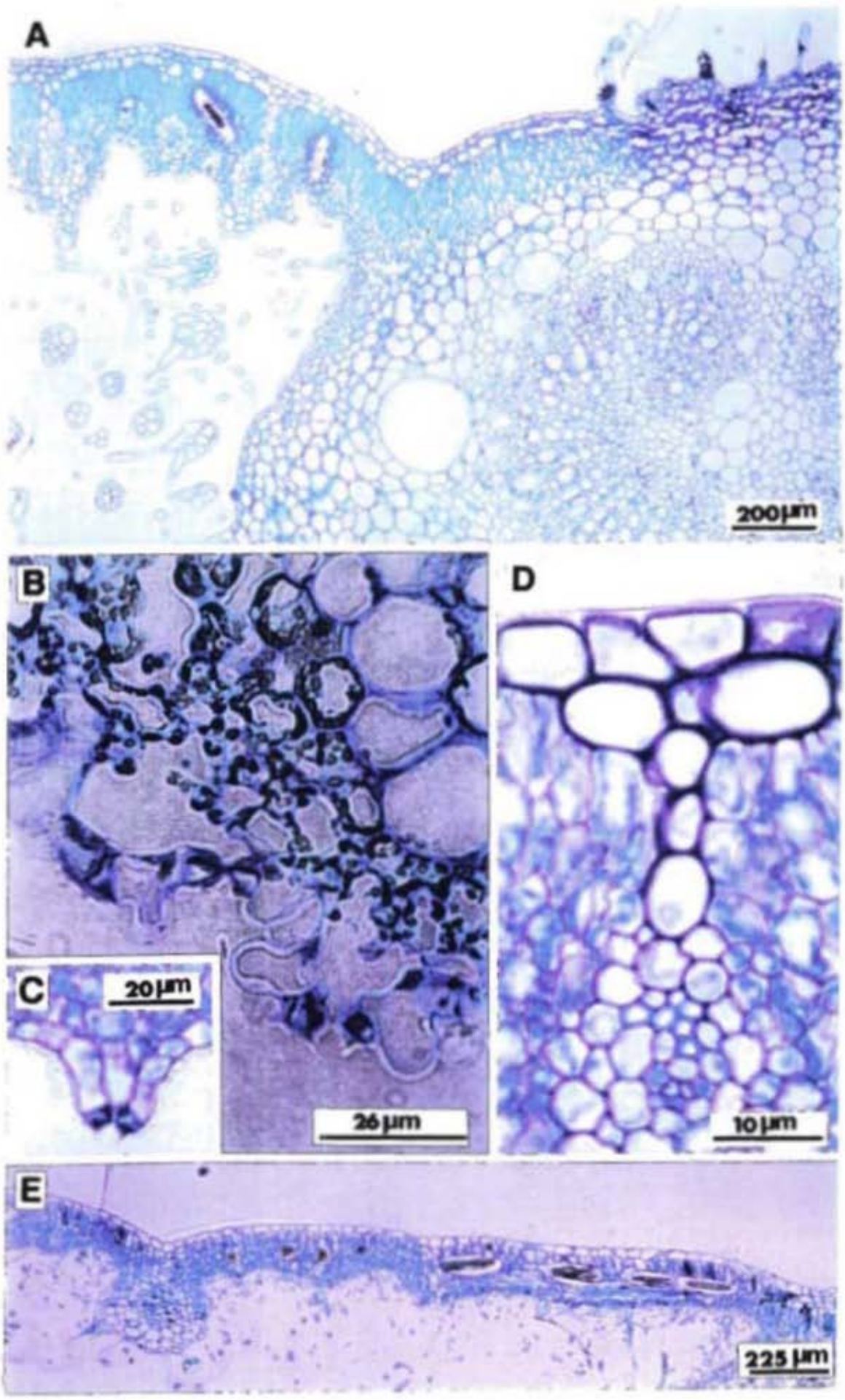

A
200µm
B
C
20µm
26µm
D
10µm
E
225µm

Table 2.15(a) Leaf anatomy of some *Actinidia*

Taxon	Abundance of epidermal hairs	Interveinal hypoderm	Number of palisade layers	Ratio of palisade to leaf thickness	Leaf thickness range intervein to 1° vein (μm)	Thickness ratio 1° vein: intervein
A. arguta var. *arguta*	rare to absent	absent	2	0.25	300 - 1140	3.8 : 1
A. arguta var. *cordifolia*	rare to absent	absent	2	0.50	270 - 1140	4.2 : 1
A. rufa	common	absent	2	0.75	225 - 2400	10.7 : 1
A. melanandra var. *melanandra*	rare to absent	absent	2	0.25	300 - 3000	10.0 : 1
A. kolomikta	rare to absent	absent	1	0.25	180 - 1260	7.0 : 1
A. polygama	rare to absent	absent	1	0.25	180 - 1950	10.8 : 1
A. valvata	rare to absent	absent	2	0.50	360 - 2400	6.6 : 1
A. callosa var. *henryi*	rare to absent	absent	2	0.25	600 - 2100	3.5 : 1
A. chrysantha	rare to absent	absent	2	0.50	300 - 1980	6.6 : 1
A. indochinensis	rare to absent	absent	2	0.25	300 - 1200	4.0 : 1
A. melliana	rare to absent	absent	1	0.25	300 - 3600	10.0 : 1

Table 2.15 continued....

Table 2.15(a) Continued.....

Taxon	Abundance of epidermal hairs	Interveinal hypoderm	Number of palisade layers	Ratio of palisade to leaf thickness	Leaf thickness range intervein to 1° vein (μm)	Thickness ratio 1° vein: intervein
A. hemsleyana var. *hemsleyana*	rare to absent	absent	2	0.50	150 - 3000	20.0 : 1
A. latifolia	common	present	2	0.75	120 - 1860	15.5 : 1
A. eriantha	common	absent	2	0.75	150 - 1560	10.4 : 1
A. chinensis var. *chinensis* 3/6/14b**	common	absent	2	0.75	210 - 1800	8.5 : 1
A. chinensis var. *chinensis* 460.4**	common	absent	2	0.75	210 - 2250	10.7 : 1
A. chinensis var. *chinensis* 460.9 **	common	absent	2	0.75	210 - 2250	10.7 : 1
A. deliciosa var. *deliciosa* 'Hayward'	common	absent	2	0.75	210 - 3000	14.2 : 1
A. deliciosa var. *deliciosa* 'Matua'	common	absent	3	0.75	330 - 3300	10.0 : 1
A. deliciosa var. *deliciosa* 'Bruno'	common	present, sparse	2	0.75	270 - 2750	10.0 : 1
A. deliciosa var.*chlorocarpa*	common	absent	2	0.75	150 - 2040	13.6 : 1

Table 2.15 continued....

Footnote : ** Numbers are different genotypes

Table 2.15(b) Leaf anatomy of some *Actinidia*

Taxon	Adaxial bundle collenchyma	Lamina horizon of 1° bundle horizon	Shape of petiole bundle near leaf base	Number of layers of sclerenchyma 1° vein (μm)	Abundance of phenolics near 1° vein	Type(s) of ergastic crystals
A. *arguta* var. *arguta*	absent	level	arc	1 - 2	rare to absent	raphides
A. arguta var. *cordifolia*	absent	level	arc	1 - 2	rare to absent	raphides cubic*
A. rufa	absent	above	arc to ring	1 - 3	common	raphides cubic*
A. melanandra var. *melanandra*	absent	level	arc	1 - 2	rare to absent	raphides
A. kolomikta	absent	above	arc	0	rare to absent	raphides
A. polygama	absent	level	arc	0	rare to absent	raphides
A. valvata	absent	level	arc	1 - 2	rare to absent	raphides
A. callosa var. *henyri*	absent	level	arc	2 - 4	rare to absent	raphides
A. chrysantha	absent	level	arc	1	common	raphides
A. indochinensis	absent	level	arc	2 - 4	common	raphides
A. melliana	absent	above	arc	1	rare to absent	raphides
A. hemsleyana var. *hemsleyana*	absent	above	arc	1	rare to absent	raphides

Table 2.15 continued

Table 2.15(b) Continued....

Taxon	Adaxial bundle collenchyma	Lamina horizon of 1° bundle horizon	Shape of petiole bundle near leaf base	Number of layers of sclerenchyma 1° vein (μm)	Abundance of phenolics near 1° vein	Type(s) of ergastic crystals
A. latifolia	present	above	circle	1 - 4	rare to absent	raphides cubic*
A. erianthia	present	above	circle	3 - 6	rare to absent	raphides cubic*
A. chinensis var. *chinensis* 3/6/14b**	present	above	circle	2 - 4	rare to absent	raphides cubic*
A. chinensis var. *chinensis* 460.4**	present	above	circle	2 - 4	rare to absent	raphides cubic*
A. chinensis var. *chinensis* 460.9**	present	above	circle	2 - 4	rare to absent	raphides cubic*
A. deliciosa var. *delicisoa* 'Hayward'	present	above	circle	2 - 3	rare to absent	raphides cubic* styloids
A. deliciosa var. *deliciosa* 'Matua'	present	above	circle	1 - 4	rare to absent	raphides cubic*
A. deliciosa var. *deliciosa* 'Bruno'	present	above	circle	2 - 4	rare to absent	raphides cubic*
A. deliciosa var. *chlorocarpa*	present	above	cordiform	2 - 4	rare to absent	raphides cubic*

Table 2.15 continued....

Footnotes : * Cubic when seen in cross-section
** Numbers are different genotypes

Table 2.15(c)

Taxon	Air spaces of spongy mesophyll	Shape of arm parenchyma	Abaxial epidermal surface	Stomatal protuberance
A. arguta var. *arguta*	well-developed diffuse	attenuated	smooth	not raised
A. arguta var. *cordifolia*	well-developed diffuse	attenuated to globose	smooth	not raised
A. rufa	well-developed diffuse	attenuated	papillate	raised
A. melanandra var. *melanandra*	well-developed diffuse	attenuated	smooth	not raised
A. kolomikta	well-developed diffuse	globose barely developed	smooth	not raised
A. polygama	well-developed diffuse	attenuated	smooth	not raised
A. valvata	well-developed diffuse	attenuated	smooth	not raised
A. callosa var. *henryi*	well-developed diffuse	attenuated	smooth	not raised
A. chrysantha	well-developed diffuse	attenuated	papillate	sunken

Table 2.15 continued....

Table 2.15(c) Continued.....

Taxon	Air spaces of spongy mesophyll	Shape of arm parenchyma	Abaxial epidermal surface	Stomatal protuberance
A. indochinensis	well-developed diffuse	attenuated	papillate	sunken
A. melliana	well-developed diffuse	attenuated	smooth	not raised
A. hemsleyana var. *hemsleyana*	well-developed diffuse	globose	smooth	not raised
A. latifolia	well-developed diffuse	globose, very poorly developed	barely papillate	raised
A. eriantha	well-developed diffuse	globose, barely developed	slightly papillate	raised
A. chinensis var. *chinensis* 3/6/14b**	well-developed diffuse	globose, barely developed	papillate	raised
A. chinensis var. *chinensis* 460.4**	well-developed diffuse	globose, barely developed	papillate	raised
A. chinensis var. *chinensis* 460.9**	well-developed diffuse	globose, barely developed	papillate	raised
A. deliciosa var. *delicisoa* 'Hayward'	well-developed diffuse	globose to attenuate	papillate	raised
A. deliciosa var. *deliciosa* 'Matua'	well-developed diffuse	globose to attenuate	papillate	raised
A. deliciosa var. *deliciosa* 'Bruno'	well-developed diffuse	globose to attenuate	papillate	raised
A. deliciosa var. *chlorocarpa*	well-developed diffuse	globose to attenuate	papillate	raised

Footnotes : * cubic when seen in cross-section, 1° vein = primary vein
** numbers are different genotypes

2.3.5 Cluster analysis of summer shoot characters

The 57 characters derived from summer shoots and used in cluster analysis are described more fully in Sections 2.2.3 - 2.2.4 of the text. The characters selected and coded for cluster analysis are listed in Appendix 2.2.1.

2.3.5.1 *Clustering by average linkage method*

Clustering by average linkage (U.P.G.M.A.) generates cohesive groupings with a minimal number of outliers (Figure 2.16).

The O.T.U.s (taxa) separate into four distinctive clusters "A" to "D" at a similarity level of 0.57 with *A. hemsleyana* and *A. melanandra* emerging as outliers, which unite with groups "B" to "D" at low similarity levels of *ca.* 0.57 and 0.50, respectively.

Cluster "A" forms at a similarity level of 0.65 and includes subclusters "1" and "2". Subcluster "1" joins at a similarity of 0.85 and comprises three replicated genotypes of *A. chinensis* var. *chinensis* as group "a", together with three horticultural cultivars of *A. deliciosa* var. *deliciosa* in group "b". The staminate cultivar 'Matua' joins the two remaining cultivars at a similarity level of 0.90.

Subcluster "2" forms at a lower similarity level of 0.86 and includes *A. latifolia* and *A. eriantha.*

Cluster "B" arises at a similarity level of 0.60 and includes two very similar plants *A. chrysantha* and *A. indochinensis* in subcluster "3", together with *A. melliana* at a much lower level of similarity.

Cluster "C" consists of *A. rufa* and *A. callosa* var. *henryi*, which join one another at a similarity of 0.60.

Cluster "D" arises at a similarity level of 0.56 and includes two subunits. Subcluster "4" includes two infraspecific taxa of *A. arguta*, *viz:* varieties *arguta* and *cordifolia.* Subcluster "5" comprises the closely related pair of species *A. polygama* and *A. valvata* in group "a", together with *A. kolomikta* at a similarity level of 0.70.

A. hemsleyana combines with cluster "D" at a low similarity of 0.55 and *A. melanandra* is the most distinctive plant of this assemblage, joining with clusters "B" to "D" at a similarity level of 0.50.

2.3.5.2 *Clustering by single linkage method*

Clustering by the method of single linkage (Figure 2.17) produces some cohesive groupings with "chaining" evident at lower levels of similarity and more "outliers" are generated than in average-linkage clustering.

Table 2.16 Linkage coefficients (average)

	OTU	Linkage coefficient
16	Chin460.4	0.9733
17	Chin460.9	0.9606
15	Chin3/6/14b	0.8624
18	AdelBruno	0.9153
19	AdelHay	0.8948
20	AdelMatua	0.8452
21	AdelChlorocarpa	0.6390
13	Latif	0.7631
14	Erian	0.3621
9	Chrys	0.8441
10	Indoch36/3/11a	0.5999
11	Mell	0.5145
3	Rufa	0.5957
8	Callhen	0.5480
1	Argarg	0.7197
2	Argcord	0.6460
6	Polyg3/12/11	0.8147
7	Valv	0.7081
5	Kolom	0.5622
12	Hemsley	0.4935
4	Melan	0.0000

Cophenetic correlation = 0.942

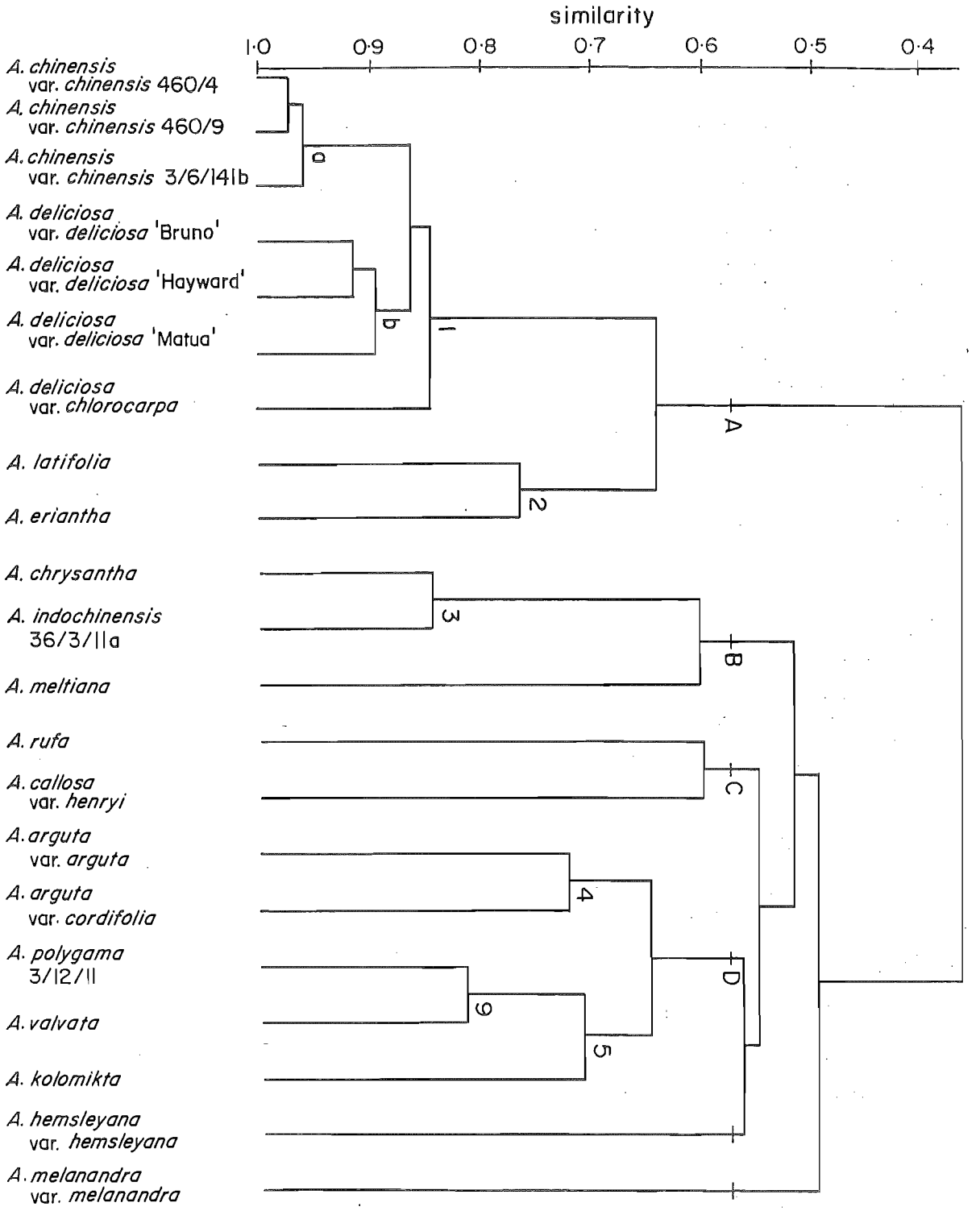


Figure 2·16: Cluster analysis of summer shoot characters using average-linkage

Table 2.17 Linkage coefficients (single)

	OTU	Linkage coefficient
16	Chin460.4	0.9733
17	Chin460.9	0.9606
15	Chin3/6/14b	0.8742
18	AdelBruno	0.9153
19	AdelHay	0.9037
20	AdelMatua	0.8659
21	AdelChlorocarpa	0.6931
13	Latif	0.7631
14	Erian	0.5293
9	Chrys	0.8441
10	Indoch36/3/11a	0.6219
1	Argarg	0.7197
2	Argcord	0.6875
6	Polyg3/12/11	0.8147
7	Valv	0.7175
5	Kolom	0.6574
8	Callhen	0.6068
3	Rufa	0.6057
11	Mell	0.6015
12	Hemsley	0.5298
4	Melan	0.0000

Cophenetic correlation = 0.919

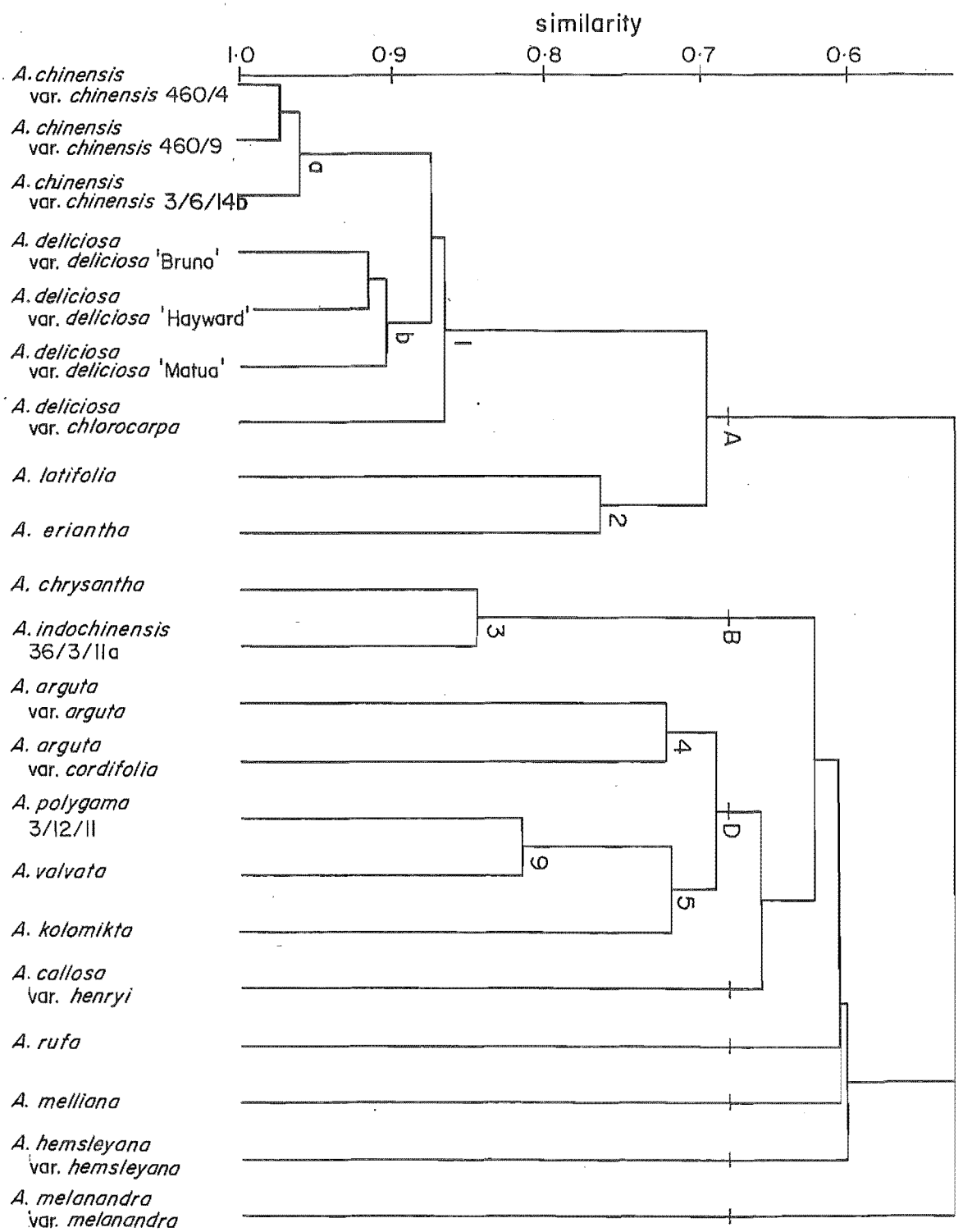


Figure 2·17: Cluster analysis of summer shoot characters using single - linkage

The composition of groups "A" and "D" is identical to that of the clusters derived from average-linkage clustering (Figure 2.16). Most of the groups, however arise at higher levels of similarity than in the former dendrogram (Figure 2.16), particularly those within clusters "A" and "D".

A. rufa and *A. callosa* var. *henryi*, formerly of cluster "C", now join the *Leiocarpae* and *A. hemsleyana* in cluster "D". *A melanandra* is still the most distinctive plant in terms of its summer shoot characters.

2.3.6 **Discriminant analysis of selected summer shoot characters**

Discriminant analysis (D.A.) is used in this chapter to test the validity of specified groups and to determine the extent to which "suitable" (continuous) characters separate these groups.

2.3.6.1 *Validation of "a priori" groups*

As in Chapter 3, groups generated from cluster analysis are chosen *a priori* as groups for D.A. Clusters "A" and "D" (Figure 2.16) include members of Sections *Stellatae* and *Leiocarpae*, respectively. Other clusters are not tested with D.A., because their composition is less explicable and their membership is not consistent between different phenograms (Figures 2.16 and 2.17). D.A. is used, therefore, to test the hypothesis that the two *a priori* groups (Clusters "A" and "D") are valid. Other groups could have been tested as predicted by Liang (1984), but my results did not justify such strategies.

The group validation procedure reveals two groups in the data set, whose membership agrees with that of the hypothesised groups. O.T.Us (individuals in effect) "1" to "7" enter the first discriminant group (= *Leiocarpae)* and OTUs "13" to "21" enter the second (= *Stellatae*).

As there are two *a priori* groups, there is only one (n-1) canonical variate (= axis), presentation of an ordination diagram (such as Figure 3.9) is not appropriate.

2.3.6.2 *Discriminant efficacy of selected summer shoot characters*

Twelve out of the 57 summer shoot characters are suitable for D.A. (for further explanation see materials and methods 2.2.10 and Chapter 3, Section 3.3.3.2).

The "discriminant efficacy" (= group separating ability) of the characters is ranked in descending order using the results of analysis of variance for the individual characters. The more discriminating of these characters maximises the variation between groups and minimises that within groups; by definition these

characters have the highest "F-values". Inspection of the F-values (Table 2.18) shows that the character "lamina area" separates these groups most effectively, whereas, "primary vein thickness : leaf width" gives the worst separation of groups. The last four characters do not attain statistical significance ($p > 0.05$), because there is too much variation within groups relative to that between them.

Canonical variates analysis (Table 2.18) shows how the selected characters separate the two *a priori* groups. The tabulated values of the "first axis" (= the sole canonical variate) show that the first four characters in Table 2.18 are mostly responsible for distinguishing the two groups. The first canonical variate explains 97.5% of the variation in the data set, indicating that most of the characters are highly correlated.

Table 2.18 : Statistics summarising "discriminant efficacy" of summer shoot characters

Variable or "character"	Univariate F[1,2] value	First canonical coefft stdised[3]
lamina area (cm^2)	33.307	1.477
freq. of 1° vein sclerenchyma layers	31.475	- 4.212
lamina width (cm)	25.729	- 2.316
ratio of palisade thickness to leaf thickness	23.838	3.339
weight of water in leaf (g)	20.558	- 0.608
primary vein thickness to interveinal thickness (ratio)	12.554	- 0.733
petiole length (cm)	9.201	0.651
ratio of leaf length leaf width	7.637	0.782
freq. of palisade layers	3.746 n.s.	0.340
freq. of leaf base types	1.942 n.s.	0.880
specific weight ($g.cm^{-2}$)	1.557 n.s.	- 0.251
primary vein thickness (as % of leaf width)	0.672 n.s.	0.846

Footnotes:
1. F-value = Ratio of variance of means among groups divided by mean of variances within groups.
2. Degrees of freedom : among groups = 1, within groups = 14; n.s. = not statistically significant ($p > 0.05$).
3. Stdised (= standardised) on the basis of standard deviations within groups; (coefft = coefficient), (freq. = frequency).

2.4 DISCUSSION

This discussion involves a comparison of the vegetative form of *Actinidia* cultivated in the D.S.I.R. germplasm collection with other *Actinidia* grown in the wild or under cultivation.

2.4.1 Nature of plant growth form

Although taxonomy involves the collation of data from many aspects, morphological characters constitute the principle sources of taxonomic evidence (Davis and Heywood 1963). The field botanist is often forced to rely solely on vegetative characters, especially in the case of non-flowering or deciduous plants. Although vegetative characters are inherently responsive to variations in environmental parameters, this does not invalidate their general use in taxonomy.

As early as 1894b Sargent used the overall form or "architecture" of the plant in taxonomic descriptions. Plant growth form "came of age" in 1978 with the publication of *Tropical Trees and Forests (an architectural analysis)* by Hallé, Oldeman and Tomlinson. These authors expressed the view that "shoot architecture" resulted from the realisation of genetically determined patterns of growth; involving correlated sets of structures with the final outcome (phenotype) being determined by environmental "fine tuning", through the ultimate channelling of resources to achieve plant form. Hallé *et al.* (*loc.cit.*) produced an architectural classification of plant form based on patterns of branching, growth rates and localisation of meristematic activity. The application of architectural models to vines such as *Actinidia* was not explored extensively, but these authors maintained that vines had a growth architecture which was heritable (i.e. genotypically based).

2.4.2 Architecture of *Actinidia* vines

Vines are naturally variable in form because they occupy different niches which are joined ontogenetically. The conditions experienced by shoots on the forest floor are very different from those of the canopy.

Several authors (Dunn 1911, Krüssmann 1984, Li 1952) have commented on the morphological plasticity of *Actinidia* vines, but despite this potential for "opportunistic" growth, a heritable growth form or architecture emerges.

Actinidia are distinguished from other genera of the Actinidiaceae (Liang 1984), firstly on the basis of growth form whether "lianoid" (*Actinidia* and *Clematoclethra*) or "trees" and "shrubs" (*Saurauia* and *Sladenia*); also by the

frequency and degree of fusion of the floral parts. *Actinidia* are further separated from related genera by their dioecy.

The growth form of *Actinidia* in the wild is well summarised by Stapf (1926) :

> *A. kolomikta* is essentially a shade-loving plant, climbing trees, deciduous as well as evergreen (conifer) by means of adventitious roots in the lower parts, or by the twining of long whip-like shoots higher up, or rambling after the fashion of brambles over the undergrowth, or in clearings trailing on the ground....
> Vines may form impenetrable thickets on the edges of forests or high in the tops of trees.
>
> Stapf 1926, first page

Actinidia vines attain the canopy by elbowing or twining past the shoots of other plants (Dunn 1911, Stapf 1926, *loc. cit.*). Their stems are little modified for climbing. There are not accessory spines or tendrils, resulting from reduction of leaves or stems, in contrast to other vines such as *Vitis* (Darwin 1875). The internal structure of the stem does not show the anomalies in vascular structure (e.g. subdivided xylem and anomalous cambia) characteristic of some tropical vines (Metcalfe and Chalk 1950, Metcalfe 1983). Some *Actinidia* (e.g. *A. kolomikta*) *A. kolomikta* produce adventitious roots at their nodes, usually upon contact with moist soil (Vorobiev 1939).

2.4.3 Types of shoots on *Actinidia* vines

Actinidia vines express a common range of genetically determined shoot types (Dunn 1911, Li 1952) and each of these has a characteristic potential for growth and flowering, whether grown in the wild or under cultivation. Furthermore, these shoot types persist in commercial orchards, even when vines are grafted onto alternative rootstocks.

Older wood ($\geqslant$ 2 yrs) gives rise to "water shoots" and these are long to arched in form and vigorous in growth. Juvenile characteristics (Dunn 1911) such as bright colours and thick tomentum persist along the full length of these shoots; these characters are normally confined to the distal regions of other shoots.

Most shoots on *Actinidia* vines are borne on wood which has over wintered for one season (= 2 yr wood). They are mostly "long", or "indeterminate" shoots (Wetmore and Garrison 1959), which are capable of considerable internodal elongation. These shoots may attain a final length in excess of 2-3 m.

The same (2 yr) wood also bears "short" or "indeterminate" shoots which are self-terminating, due to cessation of apical growth early in their development. These "spur" shoots are sympodial in their manner of growth, they undergo limited internodal growth, but they are very productive in terms of fruit numbers per

shoot. Unlike apples and stonefruit, kiwifruit do not form the bulk of their crop on "spur" shoots.

The distinction between "long" and "short" shoots is somewhat arbitrary, in that the apices of "long" shoots usually die on exposure to winter frosts, becoming sympodial in effect. Secondly, a continuum exists between "long" and "short" shoots on most vines (Ferguson 1984, 1990e).

The horticulturist manipulates the balance of genetically determined shoot types by pruning to distribute the fruit load evenly and maximally over the vine. Long shoots of *Actinidia*, like those of *Vitis* tend to fruit heavily in the middle nodes. By pruning back water shoots near the base and centre of the vine, these shoots behave as "spur" shoots and they fruit accordingly (Sale 1983).

Realisation of flowering potential in a given cultivar can be modified environmentally by removing "competitive sinks" through defoliation (Brundell 1975d) or by removal of flowers, termed "thinning" (Jackson 1986).

Domestication has increased the genotypic component of fruit size in *A. deliciosa*, but the ultimate realisation of size is dependent on cultural practices (Ferguson 1990c), particularly the availability of water (Lees 1982). The growth form of the fruit is sufficiently stable to enable species (Liang 1984, Vorobiev 1939) and cultivars (Astridge 1975, Mouat 1958; Zhang and Thorp 1986) to be identified using fruit shape, however infraspecific variation can be considerable.

Vines raised from seed in the germplasm collection of N.Z. have growth forms and shoot morphologies which are comparable with those grown in the U.S.A. (Fairchild 1927), the U.K. (Bean 1972) and China (Li *et al.* 1987). The growth form of the lianoid is more opportunistic than that of other plants. Genetic control of plant form, therefore, cannot be total.

Forest vines such as *Actinidia* need to gain considerable stature as they are not tolerant of excessive shade and the plants are not self-supporting. These vines must respond rapidly to the proximity of other plants which provide "supportive-footholds" in the forest environment. The life-form of *Actinidia* is genetically-determined, in that it is expressed consistently between generations, the mode of climbing is conservative; the complement of shoot types is uniform and the "general form" of the plant is mostly predictable under specified habitats, e.g. open forest glades, semi-shaded forest and "tree-top" tiers.

An elegant test of the heritability of plant form would be provided by morphological comparisons between hybrids and their known parents. Fairchild (1927) documented the results of a controlled cross between an *A. arguta* female and an *A. chinensis* male. Photographs of the hybrid and its parents (Figure 7) show that the hybrid is intermediate in terms of its phyllotaxis, leaf angle in

relation to petiole; density of nodes per m of shoot and leaf sizes. Further comparisons of hybrids and parents should be undertaken to assess heritability of plant form in these vines.

2.4.4 Stress-induced morphology

Kolbasina (1963) has shown that the genotypic control of plant form in *Actinidia* is not absolute. Specimens of *A. hemsleyana* (Dunn 1908) and *A. kolomikta* (Kolbasina *loc. cit.*) growing in the open on dry mountain slopes may adopt a shrubby or "bush-like" form because internodes fail to elongate. This aberrant form is also seen where *A. kolomikta* grows at the upper limit of its altitudinal range (Vorobiev 1939).

The "bush-like" form probably results from failure of the plant to fulfil the lianoid growth form, due to insufficient resources. The following experiments are needed to distinguish whether or not the bush form is genetically or environmentally determined. If "bush-like" plants were transplanted to an experimental garden at sea level, or grown from seed under favourable conditions, disappearance of the bush-form would suggest that it is environmentally determined. Its persistence under such "uniform" conditions for one or more generations, would imply that the bush form was part of the genetically determined architecture of the vine.

2.4.5 Plant size and vigour

Plant size is commonly employed in taxonomic descriptions of *Actinidia* e.g. (Liang 1984, Rehder 1951). Undoubtedly it is highly phenotypic, since size is the net result of the plant obtaining resources from the environment. Ferguson (1990a) has noted the regional differences in the size of *A. kolomikta* plants grown in N.Z., the U.K. (Bean 1972) and Eastern Asia (Kolbasina 1963).

Plant size is also dependent on the age of the specimen described. Vasiliev (1961) observed an enormous *A. arguta* plant (28 yrs old) which had a diameter of 17 cm at chest height, a projected surface area of 48 m^2 and a stature in excess of 25 m. This vine was more than 4-6 times its normal size in the wild (Rehder 1951). Taxonomic problems associated with age can be "neutralised" by examination of plant material at equivalent stages of maturity and under uniform conditions.

Plants used in this study were grown under commercial orchard conditions (Ferguson 1990c) as part of a germplasm collection. Here, the above-ground (= shoot) biomass is replaced every 2-3 yrs by pruning, to maximise the density of fruiting wood. Thus descriptions of 1-2 yr old shoots in this study are comparable

to those from plants grown in the wild.

Comparisons of leaf size data obtained from the N.Z. germplasm plants (Appendix Table 2.1.3), with descriptions of plants derived from the wild in China (Liang 1984, in Appendix Table 2.1.4.) suggest that most of the plants in N.Z. are larger and are receiving more favourable growing conditions, than those in the wild. The small size attained by the N.Z. plant of *A. kolomikta* has resulted in shorter, wider leaves than those of the Asian herbarium specimen CHR 445031.

Exemplars of *A. deliciosa* and *A. chinensis* (Appendix Table 2.1.3) obtained from the N.Z. germplasm collection are twice as large as those described from the wild (Liang 1984, Appendix Table 2.1.4). Most of the herbarium specimens listed in Appendix Table 2.1.3 were collected from the research orchard of the Guangxi Institute of Botany, but these plants are comparable in size with those of the wild. This probably reflects the superior cultural methods used in the D.S.I.R. research orchard (Ferguson 1990c).

A genetic component of plant size emerges in descriptions of *Actinidia* growing in the wild (Liang 1984, Rehder 1951, Sargent 1894a) and those from germplasm collections at Guangxi (Li *et al.* 1987) and in N.Z. These authors describe most *Actinidia* as small to medium-sized vines which mostly attain a stature of 4-6 m in the wild (Rehder 1951), with some *Stellatae* attaining a height of 8 m. Size is one of the major criteria used to distinguish *A. chinensis* var. *chinensis* from *A. deliciosa* (Liang 1975, Ferguson 1990b).

A. deliciosa is probably one of the more rampant vines (Li *et al.* 1987, Liang 1984), which maintains its vigour even after grafting and pruning in the orchard (Ferguson 1990c), and in the artificially controlled environment of tissue-culture (Gui 1981).

Dwarf forms of *Actinidia* have been described recently by Dawes (1977) and the Hunan Agricultural Institute (cited in Ferguson 1990a). The *A. chinensis* dwarf "Dongshan Feng heavy cropping dwarf No. 13", has the same genetically determined growth pattern of a wild plant, but it differs from the latter in a lack of vigour. The genotypic control of dwarfism deserves more research, as the present yields of these dwarf plants are not commercially sustainable. Dwarf plants could reduce labour costs associating with pruning in the long term.

2.4.6 **Phenology**

Most *Actinidia* described as deciduous or evergreen in the wild (Liang 1984), grow true to form in the N.Z. germplasm collection (Ferguson 1990a) under common conditions of daylength and temperature, i.e. when removed from the photoperiodic dormancy cues in the natural environment. Some *Actinidia*, (e.g.

A. melliana) are semi-evergreen in their behaviour. Further research is needed here, since Westwood notes that :

> Some deciduous species at low elevations in the tropics tend to be semi-evergreen, because they do not receive the proper environmental cues to drop their leaves and go dormant.
>
> Westwood 1988, page 24.

Flowering times are probably under environmental control, since the same taxon in different latitudes flowers at different times (Liang 1984).

2.4.7 Juvenile shoot characters

Actinidia shoots of the current years wood express a common ontogenic sequence of juvenile characters. Invariably, the distal 0.3 m of a shoot is clothed with simple pubescence which soon abscises giving the shoot a "powdery" appearance. The colour and qualities of these hairs are useful adjuncts in taxonomy. Anthocyanins in the hairs and stems impart a red-to brown colour to the tip of the shoot. Leaf shapes of the distal shoot region change from lanceolate, to ovate or widely ovate, depending on the taxon. *A. deliciosa* still expresses this pattern of leaf shape change when transferred to controlled-environment conditions (Lionakis and Schwabe 1984b), so that this is genotypic variation.

Seedling morphological characters such as dimensions of roots, stems and leaves; colour, leaf hair qualities and young leaf shape were also used to identify *Actinidia* seedlings in the germplasm collection at Guilin (Li *et al.* 1987). These authors did not detect differences in the growth forms of seedlings, in contrast to the study of conifer seedlings by Philipson and Molloy (1990). Many of the morphological characters expressed by *Actinidia* seedlings are reiterated in the growth of adult shoots (see Liang 1984).

2.4.8 Determinants of three-dimensional form of leaves

The three-dimensional form of leaves is controlled by several factors. It results from a combination of : the spatial arrangement of leaves in the bud (termed vernation), the subsequent rolling or folding of leaves in the bud (termed ptyxis) and the manner of growth of the emergent leaves. Davis and Heywood (1963, page 149) state that ptyxis and vernation are confused and underused by taxonomists in general.

Plant descriptions by Chinese authors such as Liang (1984) rely heavily on data collated from herbarium specimens (Ferguson pers. comm.), as collecting trips are few and the Chinese terrain is not easily accessible (Ferguson 1983).

My observations show that *Actinidia* can be identified on the basis of their leaf form, whether planar (e.g. *Stellatae*) or markedly arched and corrugated (e.g. *Leiocarpae*). These characters are absent from most diagnoses of the genus (Dunn 1911, Li 1952, Liang 1984). Chinese taxonomists have addressed some of the consequences of "morphology arising with the bud", in their descriptions of leaf margins, whether revolute or undulating. Major differences in folding of leaves are not apparent from dissections of *Actinidia* buds (Chapter 3). In taxa such as *A. deliciosa*, where the "bud leaves" are well separated from one another by thick layers of lanate hairs, the leaves are planar on emergence. The converse applies for *A. kolomikta* and other *Leiocarpae*.

Bullation in the leaves of many *Actinidia* arises in part from intercalary growth of lamina tissues, which are interposed between the thick and inelastic veins, especially the percurrent tertiary veins. Growth of the leaf accounts for the general tendency of *Actinidia* leaves to become planar with age. Leaves of a species look the same because they adopt the same pattern of growth. Most apical leaves are lanceolate because the primary vein grows first (Isebrands and Larson 1980) and subsequent growth of the leaf proceeds initially with expansion of the lateral veins and later with an intercalary phase of growth (see refs in: Hickey and Wolfe 1975, page 540, Esau 1965, Kaplan 1971, 1973, Pray 1955, 1963). The relative importance of growth in leaf width relative to length, characterises *Actinidia* at the section level.

Leaf shape of *Actinidia* species is genetically stable as shown by comparisons of plants grown in germplasm collections (Li *et al.* 1987 and Condon Chapter 2 of this thesis) with those in the wild (e.g. Liang 1984, Gui 1981). The genetic control of leaf shape is not as rigid as in some taxa, as it involves a spectrum of forms. There is evidence of heteroblastism in some *Stellatae*, since in *A. deliciosa* mature leaves of "long" shoots are ovate (see also Zhang and Thorpe 1986), but mature leaves of "short" shoots are orbicular. The heteroblastic expression of leaf form is part of the "correlated set of characters" such as growth rate, internode length, and fruiting potential which define the different types of shoots on the vine.

Leaf apices are variable in most *Actinidia* species and mainly involve variations of the acute or acuminate types (Liang 1984). Acuminate tips in leaves have been interpreted as "drip-tips" (e.g. Dean and Smith 1978) which are known to facilitate water run-off in high rainfall areas. *A. chinensis* is distinguished from the related species *A. deliciosa* by the emarginate leaves and the lower percentage of acute apices on older shoots (Gui 1981).

The variability of leaf base types is diagnostic of *Actinidia* species, for example *A. eriantha* has five types of leaf base, whereas *A. deliciosa* has only one: i.e., the cordate base which typifies section *Stellatae* (see also U.P.O.V. 1981).

Zhu (1983) states that shoots of *A. chinensis* have a "2 by 6" phyllotaxy. Pulawska (1965) shows that the phyllotaxis of "long-shoots" in *A. arguta* varies throughout the growing season and depends on the rates of growth of leaves and primordia. Primordial growth is dictated by acropetally directed procambial strands which originate from the bases of older leaves. Early in the spring primordia are initiated from procambial strands arising 8 leaves below the apex. Later in the season the 13th and 21st leaves below the apex initiate primordia. The developmental variability associated with phyllotaxis in *Actinidia* together with the heterogeneity induced by pruning practices, justified exclusion of phyllotaxis from this study.

The three-dimensional attainment of leaf form can also be explained in terms of "biomechanical constraints" as defined by Givnish and Vermeij (1976). These authors argue that the evolution of large planar leaves is not possible without increased investment of biomass into supportive tissues, such as leaf veins or petiole. Once leaves exceed a "critical size", the petiole must attach nearer the "centre of gravity" of the leaf and this is correlated with the development of cordate or saggitate types of leaf bases (e.g. *A. deliciosa*).

2.4.9 Upper (Adaxial) leaf surface

Leaf reflectance or "gloss" depends on the thickness and composition of the cuticle (Martin and Juniper 1970). Thick glossy cuticles such as those of *A. arguta* and *A. melliana* may be related to the need to conserve water in the wild. Physiological measurements of cuticular transpiration could confirm this hypothesis. Leaf "gloss" is also preserved in some herbarium specimens of *A. arguta* (e.g. CHR 381774A).

The adaxial surface is green in leaves of most *Actinidia*, with variations arising from the nutritional status or the genetically determined density of chloroplasts beneath the epidermis. Cultivars of *A. deliciosa* can be separated on the basis of their leaf colour in the *Actinidia* germplasm collection; some species such as *A. eriantha* have distinctively "grass green" leaves.

Leaves of some *Leiocarpae* (e.g. *A. polygama; A. kolomikta*) can be spectacularly variegated when exposed to light (Fujita 1935, Kuster 1928, 1933, Krüssman 1984). This variegation is not restricted to male plants (Michurin 1949,

Vorobiev 1939) as Krüssman *loc. cit.* and Stapf (1926) have suggested. Variegation is maintained by failure of chloroplast development and may not persist under low-light conditions (Fujita 1935, Kolbasina 1963).

2.4.10 **Lower (abaxial) Leaf surfaces**

Some cuticular characters of the lower leaf surface are conservative for all *Actinidia*. The cuticle is attached to the epidermis by flange-like structures (Dilcher 1974) of the cuticular membrane. Most authors (e.g. Gao 1988) fail to recognise that abaxial surfaces of these leaves have two types of stomata; those with guard cells surrounded by radiating (anomocytic) or perpendicular configurations (paracytic) of accessory cells. The stomatal apertures are larger in the *Stellatae*, but the length to width ratios of stomatal apertures are not stable at species level.

2.4.11 **Types of leaf hairs (trichomes)**

Li (1952) emphasised the importance of foliar hair types in his taxonomic revision of the genus. Liang (1984) has built upon this system with the recognition of many taxa, including several new sections.

Subdivision of the genus based on the type and abundance of abaxial foliar trichomes is one of the more useful contributions of vegetative morphology to *Actinidia* taxonomy.

2.4.11.1 *Leiocarpae*

My observations of foliar trichomes in Sections *Leiocarpae* and *Stellatae*, *Perfectae*, confirm the validity and genotypic basis of the hair types as recognised by Li (1952) and Liang (1984). Our specimen of *Actinidia rufa* seems anomalous with a placement in section *Leiocarpae* as its stems are densely covered with the finely pulverent remains of simple hairs. Other *Leiocarpae* are typified by glabrous stems. This taxon has variously been treated as a variety of *A. arguta* or as a species in its own right. It was not considered by Liang (1984) as this author confined his attention to Chinese *Actinidia*.

If our specimen of *A. rufa* is correctly identified then its taxonomy needs to be reconsidered. I have not examined reproductive material, but the anthers are supposedly (Li 1952) dark in colour, which is characteristic of *Leiocarpae*. Of greater importance however is the condition of the fruit, that is, whether it is spotted or not, The *Leiocarpae* are distinguished from other sections of the genus by their non-lenticellate or "immaculate" fruit. One way to resolve this dilemma is to examine Japanese herbarium specimens (collected from the native habitat) and compare them with the N.Z. plant. This would at least rule out the possibility of a misidentification.

2.4.11.2 *Maculatae*

Section *Maculatae* Dunn is defined by the presence of glabrous or glabrate plants, in conjunction with "spotted" or lenticellate fruit. Unfortunately, fruit are spotted in three quarters of the genus, so the "marker" character defining this section of the genus is not distinctive. Other characters defining the *Maculatae* are equally widespread amongst other sections of the genus and within this group, the range of expression of these characters is variable, for instance :

> Half of the species have hairy sepals and the other half are glabrous.....
> The ovaries are cylindrical or globose.....
> The pith is lamellate or solid.....
> and most species have glabrous branches, petioles and lower surface of leaves.
>
> Liang 1984 [translation].

A. chrysantha, *A. indochinensis* and *A. callosa* var. *henryi* conform to the "general sense" of this group. My specimen of *A. callosa* var. *henryi* possesses red, stellate hairs in the axils of secondary veins of the leaf underside. This observation is disturbing, since this character is supposed to be unique to members of section *Stellatae* (Li 1952, Liang 1984). These stellate hairs have a variable number of branches. This is in contrast to the generally fixed number of branches in hairs of the *Stellatae*, Series *Perfectae*, which I have examined. *A. callosa* is a large and widely distributed species which, according to Liang (1983), has a "strong influencing power" over the whole section. Further evidence of branched (not simple) hairs of *Maculatae* comes from examination of Chinese herbarium specimens, collected and determined by Liang in Guangxi. In *A. cylindrica* var. *reticulata* (CHR 422 183) abaxial hairs are fine in cross section and cascading in their form. However, they range in complexity from bifids to quadrifids (two and four armed hairs). The branches of these hairs do not arise from pedicellate stalks as in many *Stellatae*; instead the hairs branch from the base like those of *A. eriantha*.

2.4.11.3 *Strigosae*

Members of this section have simple (not stellate) pubescence on the undersides of leaves; shoots are covered with yellowish or brownish strigose hairs, with more or less setose hairs on one or both surfaces (Li 1952, page 5).

Like Stace (1965) I find the use of some terms such as "strigose" to be rather subjective. There is a need for international nomenclature such as that adopted for leaf shape (S.Y.S.T.A.N.Z. 1962). Ideally, taxonomic characters which delimit important categories such as sections should be demarcated using

unambiguous characters. Provided their meaning is clear, terms such as "setose" describe correlated sets of attributes (e.g. relative size, orientation and shape of hairs) and are therefore concise.

Examination of Chinese herbarium and N.Z. specimens of *A. hemsleyana*, show that the abaxial surfaces of leaves are covered with bristle-like trichomes, most of which are bifids. According to Liang, (1984, diagnoses [translated] page 11), the hairs are not branched and hispid, hirsute or setose.....Again I question the observations of Li (1952) and Liang (1984). It is necessary, however, to examine the plants with high power stereoscopic or scanning electron microscopes to be certain about the morphology of the trichomes.

2.4.11.4 *Stellatae*

There are few problems with the identification of members of Section *Stellatae*, series *Perfectae*, either from my own or the Chinese herbarium specimens (Appendix Table 2.3.1) consulted.

The non-stalked, stellate hair type, as in *A. eriantha* (see also Gao 1988), however is little removed from some of the more complex quadrifids or other branched hairs of some *Maculatae* and *Strigosae*.

I wish to draw attention to possible anomalies in members of Section *Stellatae*, series *Imperfectae*. In these taxa the lower surface of the leaves are either densely covered with imperfectly stellate hairs, or are sparsely covered with caducous (non-persistent) hairs. Many members of this section appear morphologically similar to plants from other sections of the genus.

Liang's remarks on *A. pilosula* are worth quoting :

> This species is close to *A. venosa* but it is more hairy and with more flowers. There are many branched pilose hairs on the lower surface of the leaves and the young branchlets and petioles are also hairy. Thus it seems distant from typical members of the *Maculatae* and looks to be an intermediate type between the *Maculatae* and *Stellatae*.
>
> Liang 1984 [transl.], page 77

A. obovata is supposed to be morphologically similar to *A. callosa* var. *henryi*. This is interesting in view of my observations on the branched hairs of the latter. Could it be that *A. callosa* var. *henryi* might also have "imperfectly stellatae" hairs? I suspect that many of the branched hair types seen in the *Maculatae* might also be regarded as imperfectly stellate. I can not challenge the validity of Section *Stellatae*, *Imperfectae* until I have examined herbarium specimens, but unfortunately none of these are avaialble in N.Z.

Either the trichomes are reliable taxonomic characters, which accurately

reflect the complex evolutionary and geographic history of the genus (Liang 1983), or the trichomes themselves are dubious characters. At present I favour the former hypothesis. But this is a complex issue, since validation of these sections would require cladistic studies using independent lines of cytotaxonomic and chemical data (Jones and Luchsinger 1980). Regretably, such studies are beyond the scope of this exploratory investigation. There is sufficient evidence at present, to prompt a complete revision of *Actinidia* taxonomy at the section level.

2.4.12 Leaf venation

The pattern of correlated characters of leaf venation, termed leaf venation architecture (Hickey 1973, 1979), can be used to identify *Actinidia* at the generic or sectional level. The conservative nature of many of these characters has led to attempts at phylogenetic classifications, e.g Hickey and Wolfe (1975).

Actinidia leaves are simple in form and they all have pinnate venation, opposite secondary veins and strongly percurrent tertiary venation (Hickey and Wolfe 1975, pages 563-565). The progression from *Leiocarpae* to *Stellatae* is accompanied by: increasing "directness" of secondary venation toward the margin (semicraspedodromous to craspedodromous secondary venation), particularly the development of pectinal venation, and increased planation of the margin in conjunction with outwardly protruberant teeth. The areolation decreases in size and increases in its morphological regularity (Dilcher 1974, Hickey 1973, 1979, Gao 1988).

The major trends in leaf venation may have important implications for water-relations in these plants, particularly when *Leiocarpae* are compared with *Stellatae*. The *Leiocarpae* may have evolved in N.E. Asia where relative humidities and rainfall levels are lower than those further south (Tregear 1980). The orientation of "water-excreting" teeth (hydathodes) changes from oppressed in the *Leiocarpae* to outward in the *Stellatae*, which would be conducive to greater water expenditure in the latter group.

2.4.13 Hydathodes

Apart from an isolated report of water-glands in *A. kolomikta* (Stapf 1926), hydathodes are otherwise unknown in the genus *Actinidia*. The size and orientation of the hydathodes is intimately related to the "directness" of the marginal venation and the capacity of the veins to deliver water (e.g. primary vein and areole sizes). The existence of hydathodes in *Actinidia* is only part of a syndrome of "water-spending" characters, most of which are poorly researched. The following discussion attempts to consider possible implications arising from

exploratory observations of hydathode structure in *A. deliciosa* var. *deliciosa* cv. Hayward.

The term "hydathode", synonymous with "water-excreting" gland or tissue (Fahn 1979) should only be applied after structural and functional criteria are satisfied.

Observations of the margins of leaves in the early morning or shortly after rainfall, often show aggregations of water droplets in the margins of leaves. This response is most marked in young leaves. Elimination of water (guttation) continues for 5-10 min. when leaves are detached from the plant and examined using a stereomicroscope. Guttation does not appear to continue under conditions conducive to water deficit, such as photosynthesis at midday. Water-elimination by guttation therefore, appears to require a positive water potential, although this has yet to be quantified. Hydathodes have probably developed in the native habitat in response to high humidity (70-80%*) and high rainfall (1000-2100* mm p.a.) (*Ferguson 1984, Liao and Wang 1984).

Collectively, the structural observations in this thesis suggest that hydathodes are metabolically and ultrastructurally active throughout their life, but more so in juvenile or recently unfurled leaves. The spatial proximity of veinal terminations to the apices and stomatal chambers of hydathodes and the consistency between hydathode orientation and the directness of secondary venation, suggest that these teeth function in efficient delivery of water to the surface of the leaf.

Ultrastructural modifications toward the apical end of the vascular pathway involve: 1. expansion of the free-space continuum between cells (for storage of water), 2. increased surface area of cell walls for apoplastic transport and 3. metabolic enhancement (enhanced activity and organelle complexity) in the epithelial parenchyma cells proximal to the endpoints of the tracheids.

Epithem cells of *Actinidia* are similar to those of the hydathodes in Ranunculaceae (Perrin and Zandonella 1971), in the formation of cytoplasmic compartments by invaginations of the nucleus. These compartments may affect localisation of organelles for ion-transport and so enhance the rate of guttation. Hydathodes in *Actinidia* may not be as metabolically active as those of *Papaver* and *Taraxacum* (Perrin 1971), since transfer wall processes (cell wall ingrowths) have not been observed in the epithem cells of *Actinidia.*

The general structure of hydathodes in *Actinidia* is most reminiscent of *Physocarpus*, Rosaceae (Lersten and Curtis 1982), except that the apices of *Actinidia* hydathodes are not as complex.

The tracheids themselves have thin longitudinal walls inbetween the secondary wall thickenings and may facilitate a low resistance pathway for the outflow of water (Fineran pers. comm.).

Elimination of water is most likely to be via the stomata which occur on upper and lower surfaces of the gland, since the thick cuticle covering the epidermal walls is probably impervious to water. This hypothesis is supported by the absence of plasmodesmata in the cell walls of young hydathodes.

Important questions arise concerning the developmental fate and functional life of the hydathodes, and whether or not they are capable of controlling water-loss at times of water deficit, namely, what is the longevity of the stomata and what is the magnitude of cuticular transpiration, if any?

Physiological and further structural studies are clearly needed to evaluate the possible importance of these structures in the cultivation of *Actinidia*.

2.4.14 **Leaf anatomy**

Systematic anatomy of plants began with the work of Radkofler (1875) and reached its climax with the works of Solereder (1908) and Metcalfe and Chalk (1950). Solereder (*loc. cit.*) stressed the phylogenetic importance of environmentally-independent characters such as type of stomata, hairy coverings, and secretory tissues.

Taxonomically important characters in *Actinidia* can be assessed from the researches of Dunac (1899), Lechner (1915), Metcalfe and Chalk (1950), Gao (1988) and myself. My observations were made on plants grown in an experimental garden, where all plants were treated alike. My comparisons were based on leaves obtained from fully sunlit shoots, termed "sun-leaves" (e.g. Busgen 1929).

According to Metcalfe and Chalk (1950, page 191), the most significant character of the Actinidiaceae is the occurrence of crystalline bundles termed raphides. These occur in elongated sacs or tubes situated in the mesophyll and petiole cortex. They are usually embedded in a mucilaginous matrix like those of related families, e.g. Malvaceae. My observations show that crystals show an increase in size from the *Leiocarpae* to the *Stellatae* and that this is not generally known. Although raphides are common to all *Actinidia*, there are larger prismatic crystals of cubic cross-section as found in *A. arguta* var. *cordifolia* and in the *Stellatae*, but I did not see them in other *Actinidia*. In *A. deliciosa* there are huge solitary crystals termed "styloids" (see also Clark, Smith and Walker 1987), which fill the entire cell. Some authors fail to observe the details of crystalline structure (e.g. Gao 1988) because the matrix of the crystals is dissolved during processing for microscopy. This is not the case with freeze-dried preparations

however.

Redgewell (1983) has undertaken a chemotaxonomic survey of mucilages in some *Actinidia*. *Leiocarpae* have mucilages with a positive specific-rotation, whereas *Stellatae* have mucilages with a negative specific-rotation. Purified mucilages of *Stellatae* have higher percentages of fucose and lower percentages of mannose and glucuronic acid than those of the *Leiocarpae*. *A. rufa* also emerged with a fundamentally different mucilage composition than the *Leiocarpae*, to which it allegedly belongs. Further studies of crystal-containing cells in the genus might yield phylogenetically useful information about these plants.

Other taxonomically useful anatomical characters include palisade and mesophyll morphologies and the distribution and abundance of sclerenchyma fibres associated with the vascular bundles of the primary vein (midrib). Gao (1988) emphasised the taxonomic constancy of petiole bundle form nearest the base of the lamina and my findings confirm this. Gao (*loc. cit.*) has shown that palisade to mesophyll ratios are genetically stable (I agree) and that they are ecologically related to the requirements of these species in the wild. Gao devised a key which identifies *Actinidia* to species level based on areole characters, petiole bundle form and types of foliar trichomes. However I find Gao's use of the term "glandular trichome" to be unacceptable. Application of the term glandular (like the hydathodes) requires a demonstrable secretory function - it can not be applied to any structure with a swollen apex. The same applies to the "glandular teeth" of Hickey (1979).

2.4.15 Systematic affinities of *Actinidia (?)*

The genus *Actinidia* shares the presence of crystals, mucilage, and/or stellate hairs with several families e.g. Ericaceae, Malvaceae, Tiliaceae; Theaceae. There are also similarities in terms of: leaf venation architecture (Hickey and Wolfe 1975), sieve-element plastid type ("S-type" (Behnke 1981), and immunological cross-reactivity of proteins (Kolbe and John 1980, John and Kolbe 1980). Possible affinities suggested by vegetative characters also accord with general similarities in floral characters (see Cronquist 1981). Important evidence of "systematic affinities" also emerges from the embryological studies such as the number of integumentary layers and the thickness of the nucellus (Philipson 1974, 1977). The bitegmic, tenuinucellate ovule of *Actinidia* has led Philipson to postulate a closer relationship between the Actinidiaceae and Ericaceae than that suggested by other authors.

2.4.16 Cluster analysis of vegetative characters derived from summer shoots

Cluster "A" is a distinctive but cohesive assemblage of "large, wide-leafed" forms with widespread stellate hairs on the underside of the leaves. This corresponds to members of the *Stellatae, Perfectae* (series).

Subcluster "1" includes three genotypes of the diploid species (group "a") *A. chinensis* (2n = 2x = 58): a small smooth-stemmed plant with spherical fruit. Subcluster "1" also contains (group "b") the cultivars of the hexaploid species *A. deliciosa* (2n = 6x = 174): a large plant with hispid stems and elongate or ovoid fruit. Both of these species were formerly regarded (Liang 1975, 1982 a;b) as altitudinally separated variants of *A. chinensis*. Morphological intermediates are known where their distributions overlap (Liang *loc. cits.).*

Subcluster "2" denotes two other members of the *Stellatae* which are mainly lowland species.

The phenogram correctly depicts the high similarity values expected from closely and more distantly related species in cluster "A".

Cluster "D" is another cohesive group but it is not as compact as the former. This major cluster includes examples of Section *Leiocarpae*, which are united by their immaculate (non-lenticellate) fruit and basically glabrous shoots. This group emerges as a cohesive entity in the absence of the "non-spotted" marker character, i.e. it is a "good" group (see Chapter Four).

Subcluster "4" contains two varieties of the polymorphic and widely distributed species *A. arguta* (Li 1952, Liang 1983).

Subcluster "5" contains *A. polygama* and *A. valvata* of series *Solidae* (solid pith), together with *A. kolomikta* of series *Lamellatae*. All of these plants have adaxially variegated leaves (Krüssmann 1984, Liang 1984).

The subdivision of the *Leiocarpae* in the phenograms might be an artifact of the species chosen, but it does coincide with a discontinuity in the number of flowers per cyme, 1-3 or 1-7. Liang (1984) may have split the *Leiocarpae* in the wrong place i.e. artificially, but further lines of evidence are required to test this hypothesis, e.g chemotaxonomic data.

The composition of clusters "B" and "C" is not always consistent, so that conclusions are tentative, particularly regarding cluster "C". The association of *A. indochinensis* and *A. chrysantha* does accord with the fact that both taxa form an allopatric pair of species (Liang 1984).

The present matrix of 57 summer shoot characters may not have led to detection of *Maculatae* and *Strigosae* for several reasons :

1 The taxa chosen may not be representative of the variation defining the groups (a possibility);

2. the groups themselves may be poorly defined (a distinct possibility);

3. the choice of characters is not appropriate (unlikely since many of the characters I used are currently used by Liang (1984)to define groups).

These arguments are further explored in Chapter Four.

The phenograms presented in Figures 2.16 and 2.17 are extremely representative of the similarity matrix (Appendix 2.2.2) from which they were derived, as the cophenetic correlation coefficients are high (*ca.* 0.90).

2.4.17 Discriminant analysis of some characters from summer shoots

Most of the characters employed in this chapter are continuous, multistate or discrete in type. It is obvious how these characters distinguish the groups by examining tables of results for obvious discontinuities in character states. Discriminant analysis is used to determine the relative efficacy of continuous characters in separating the two explicible groups in this chapter *Leiocarpae* and *Stellatae*.

The dimorphic leaf bases in *Stellatae*, the development of sclerenchyma fibres and the increase in leaf: width, biomass and water content of supportive tissues distinguish *Stellatae* from *Leiocarpae*. Most of the "physiologically responsive" leaf variables such as petiole length, specific weight (Morgan *et al.* 1985) and number of palisade layers (Busgen 1929, Gao 1988) are of limited value in identification of these groups. The discriminant value of leaf size may be accentuated by the ploidy differences (McNeilage and Considine 1989) between these plants.

2.5 CONCLUSIONS

1. *Actinidia* are distinguished from other genera in the family by their habit. They are horizontal or rambling vines with a strongly opportunistic growth form. Despite the variability of these vines (Dunn 1911, Krüssmann 1984; Li 1952), there are genotypic components of growth form which are continually reiterated in the vines grown in the wild or under cultivation. These features include: climbing strategy, growth form, shoot types and growth pattern characteristics (also fruitfulness); plant size and vigour under comparable conditions, leaf size and shape and spectrum of juvenile characteristics; leaf orientation and ptyxis, leaf venation patterns - types of foliar trichomes, sclerenchyma fibres and ergastic crystals. Although the

ultimate realisation of plant form is strongly determined by environmental factors, it is basically predictable under specified habitat conditions.

2. Important "marker" characters such as trichome types used by Dunn (1911), Li (1952); Liang (1984) to demarcate sections of the genus may require revision, or some of the groups themselves may be suspect, particularly *Maculatae* and *Strigosae*.

3. The first numerical taxonomic study of part of this large and varied genus has revealed the cohesion and the distinctness of Sections *Stellatae* and *Leiocarpae*, as also shown by studies of mucilage composition (Redgewell 1983). Cluster analysis of some *Stellatae* reflects known ecological and chromosomal relationships of these taxa.

4. Hydathodes first reported in leaves of *A. kolomikta* by Stapf (1926) are shown to occur in all *Actinidia* examined and are most developed in Section *Stellatae*. The size and orientation of these "water-excreting" glands is intimately related to the directness of leaf venation (craspedodromous) and density of areolation in *Actinidia*. Hydathodes have direct central veins branching to parenchyma cells short of the surface. Epithem cells are ultrastructurally differentiated toward the tip with amoeboid-shaped secretory epithem cells near the tracheids. Enlargement of the freespace-continuum and attenuation of the lateral walls of tracheids are conducive to lateral outflow of water in this region. The structural organisation of the hydathode favours elimination of water via stomata, rather than rupture of surface cells and symplastic transport in this region is apt to be limited. The longevity and fate of hydathodes in *Actinidia* need further study.

CHAPTER THREE

COMPARATIVE (VEGETATIVE) MORPHOLOGY OF "WINTER-SHOOTS" IN SOME *Actinidia*

CHAPTER THREE

3.1 INTRODUCTION

The morphology expressed in winter shoots of *Actinidia* vines can be extraordinarily diverse (Dunn 1911). Even within the organised limits imposed during maintenance of the horticultural habit, a range of shoot types persists on the vine from "long" indeterminate shoots to self-terminating shoots arising from current year's wood, to vigorous regrowth or 'water shoots' growing from older 'leaders' on the vine. The morphology of the vine in winter results mainly from the imposition of pruning and training practices, which are designed to maximise crop yields by removal of non-flowering or previously flowering ('spent') wood (Ferguson 1990a, Sale 1985).

The current taxonomic treatment of *Actinidia* (Liang 1984) contains information on leaves, flowers and fruit, but there are little or no descriptions of winter shoot characters. This is unfortunate since most of the 50 or so species recognised by Liang are perennial, deciduous vines and identification of *Actinidia* is impossible using keys contained in *Flora Reipublicae Popularis Sinicae* in the absence of flowers, fruit or leaves. Earlier taxonomic treatments by Dunn (1911) and Li (1952) were equally deficient in this respect.

Some authors were not unaware of the value of winter shoot morphology in *Actinidia.* Poyarkova (1949) used the degree of bud protection to diagnose four species of Russian *Actinidia.* Gui (1981) stated that bud characters were the most obvious of all features distinguishing *A. chinensis* var. *chinensis* from *A. chinensis* var. *hispida* [[1]synonymous with *A. deliciosa* (see Liang and Ferguson 1984, 1986). Ferguson (1990b)] also noted that these taxa could be distinguished by the shape, height and extent of protection of their winter buds. Zhang and Thorp (1986) showed how morphological attributes such as: wood colour and texture, lenticel size, shape and distribution, bud shape and its components could be used to distinguish between twelve cultivars of *A. deliciosa*, using winter shoot material. Preliminary observations of *Actinidia* growing in the N.Z. DSIR *Actinidia* germplasm collection, suggested that winter shoot morphology might have potential for identification of other *Actinidia* species.

---

[1] The term bud-case is used throughout this thesis in synonymy with the term bud cover. Bud-case conveys the fully enclosed nature of this structure.

Internal bud structures in *Actinidia* have long intrigued morphologists such as Hildebrand (1883), Feist (1887) and Lubbock (1899). These workers showed that buds of cold-tolerant vines, such as *A. kolomikta* and *A. polygama*, consisted of incipient winter shoots, deeply concealed within a structure, formed by the combined growth of the petiole base and stem tissues (Hildebrand 1883). The external appearance of the winter bud is dominated by a smoothly rounded bud-cover of ligneous appearance. The bud case is much elongated on the basipetal side, rises short on the axillary side. The top of the bud cover, perpendicular to the axis, has a large circular scar, representing the remains of the petiole base, including its bundle trace. The incipient winter shoot is invisible from the exterior of the bud (Anon 1973), but for a minute pore through which the shoot emerges in the spring. According to Lionakis and Schwabe (1984a), the bud-cover maintains the shoot in a state of dormancy, by excluding light and oxygen and, through storage of ABA-like growth inhibitors.

Shoot structures were identified in detail by Brundell (1975a) who showed that the incipient winter shoots of *Actinidia deliciosa* cv. Hayward comprised 3-4 bud scales, 2-3 transitional (partly sclerified) leaves and 15 leaf primordia. Winter buds of kiwifruit contain only vegetative structures and no floral parts, unlike grapes (Antcliff and Webster 1955). The floral stimulus is initiated late in the growing season and formation of floral parts, term 'evocation', is delayed until 10 days before bud-break (Brundell 1975b, Ferguson and Davison 1986).

Buds on winter fruiting arms in kiwifruit vines are either 'mixed' or 'simple' (Jackson and Sweet 1972), in that they break in spring to form floral and vegetative, or solely vegetative shoots (laterals). The percentage of floral buds realised in the spring is determined by the particular cultivar (Brundell 1975c, Zhang and Thorp 1986) and the management procedures adopted by the grower (Ferguson 1990c).

International kiwifruit trade is based mainly on a single pistillate cultivar, one of 50 species of *Actinidia*, namely, *A. deliciosa* (A. Chev.) var. *deliciosa* (C.F. Liang *et* A.R. Ferguson) cv. Hayward. This cultivar has fruit of consistent ovoid shape with good keeping qualities. 'Hayward' has the disadvantages of low floral productivity, poor or uneven bud-break and late flowering. It also has a higher dormancy-breaking, or "chilling-hour" requirement, than can be satisfied in many temperate or warm temperate climates. It is therefore advisable to examine other species in the genus, to diversify the future cultivars (McNeilage and Considine 1989, Ferguson 1990d).

With these considerations in mind, the aims of this chapter are as follows :

1. Assessment of the morphological and genotypic diversity displayed by winter shoots of 20-30 *Actinidia* in the D.S.I.R. *Actinidia* germplasm collection.
2. Experimental exploration of the taxonomic potential of winter shoot characters in these *Actinidia*, with detailed examination of infraspecific variation in two horticulturally important species *viz; A. deliciosa* and *A. chinensis*.
3. Consideration of the horticultural potential displayed by winter shoots of these different *Actinidia* taxa and its possible relevance to breeding new cultivars in the future.

3.2 MATERIALS AND METHODS

3.2.1 **Collection of plant material**

Winter shoots in 0.5 m lengths were obtained from vines in the D.S.I.R. Kiwifruit germplasm collection in May of 1989. At the time of collection, buds were judged to be completely mature and fully dormant. Three to four canes were pruned from 1-2 plants of each of the 32 taxa, so that n = 10 buds were sampled from an individual plant. Material was stored at 4°C in a refrigerated cold-room for 1-3 months during the study.

3.2.2 **List of plants studied**

A list of taxa sampled from the germplasm collection with plant accession numbers is presented in Tables 3.1 and 3.2. Many of these plants were also used in Chapter Two.

3.2.3 **Descriptions of plant form**

Much of the terminology used in this thesis has been developed on an *ad hoc* basis, with some terms adapted from several sources including: Lubbock (1899), Brundell (1975a) and Zhang and Thorp (1986). In general the taxonomic literature has devoted little attention to bud structure.

A selection of genotypes was obtained from the germplasm collection to assess the range of variation exhibited by the polymorphic species *Actinidia chinensis* var. *chinensis*. Plants were selected from as broad a geographic range as possible, to enable a detailed consideration of infraspecific variation of winter shoots in one major species of the genus.

TABLE 3.1 Vines of *Actinidia* Lindl. examined.

Taxa as recognised by Li (1952), Liang (1980, 1982a,b, 1983, 1984); Liang and Ferguson (1984, 1986).
Introduction and source categories : 1 = 1904, seeds, Japan; 2 = 1955, plants, England (original source not known); 3 = 1975, seeds, China; 4 = 1977, seeds, Japan; 5 = 1977, seeds, China; 6 = 1979, scionwood, USSR; 7 = 1981, seeds, China; 8 = 1981, scionwood, China; 9 = unknown, selection of Fletcher and Mouat.

Taxon	Orchard plant number(s)	Sex M/F	Intro and Source
Genus *Actinidia* Lindl.			
Section *Leiocarpae* (Dunn) Li			
Series *Lamellatae* C.F.Liang			
A. arguta (Sieb.et Zucc.) Planch. ex Miq.			
var. *arguta*	(T.P.)4/1/4	F	2
var. *cordifolia* (Miq.) Bean	(T.P.)4/1/16	F	2
A. rufa (Sieb. et Zucc.) Planch. ex Miq.	(T.P.)3/11/8 2nd vine	M	4
A. melanandra Franch.			
var. *melanandra*	(T.P.)4/1/9a	M	2
A. kolomikta (Maxim. et Rupr.) Maxim.	(T.P.)3/11/11	?[1]	6
Series *Solidae* C.F. Liang			
A. polygama (Sieb. et Zucc.) Maxim.	(T.P.)3/12/11	M	4
	(T.P.)3/12/9a	M	4
A. valvata Dunn	(K.)M1B1	M	7
Section *Maculatae* Dunn			
A. callosa Lindl.			
var. *henryi* Maxim	(T.P.)4/2/14b	M	2
A. chrysantha C.F. Liang	(T.P.)36/3/15a	M	7
A. indochinensis Merr.	(T.P.)36/3/8b	M	7
	(T.P.)36/3/11a	M	7
Section *Strigosae* Li			
A. melliana Hand.-Mazz	(T.P.)36/3/3a	M	7
A. hemsleyana Dunn			
var. *hemsleyana*	(T.P.)3/8/19a	M	3
Section *Stellatae* Li			
Series *Perfectae* C.F. Liang			
A. latifolia (Gardn. et Champ.) Merr.			
var. *latifolia*	(K.)M5B4	F	7
A. eriantha Benth.	(T.P.)3/7/15c	F	3
Section *Stellatae* Li			
Series *Perfectae* C.F. Liang			
A. chinensis Planch.			
var. *chinensis*	(T.P.)3/6/7a[2]	F	8
	(T.P.)3/6/9a[2]	F	8
	(T.P.)3/6/14b	F	5
A. deliciosa (A. Chev.) C.F. Liang et A.R. Ferguson			
var. *deliciosa*			
c.v. Haywood	(T.P.)4/3/1	F	1
Bruno	(T.P.)4/5/16	F	1
Abbott	(T.P.)4/11/10	F	1
Gracie	(T.P.)4/2/2	F	1
Greensill (constricted)	(T.P.)4/3/9	F	1
Allison	(T.P.)4/4/12	F	1
Matua	(T.P.)4/2/16	M	9
Jones	(T.P.)4/4/14	F	1
Monty	(T.P.)4/4/8	F	1
Elmwood	(T.P.)4/4/1	F	1
var. *chlorocarpa* (C.F. Liang) C.F. Liang et A.R. Ferguson	(K.)C6M2	F	7

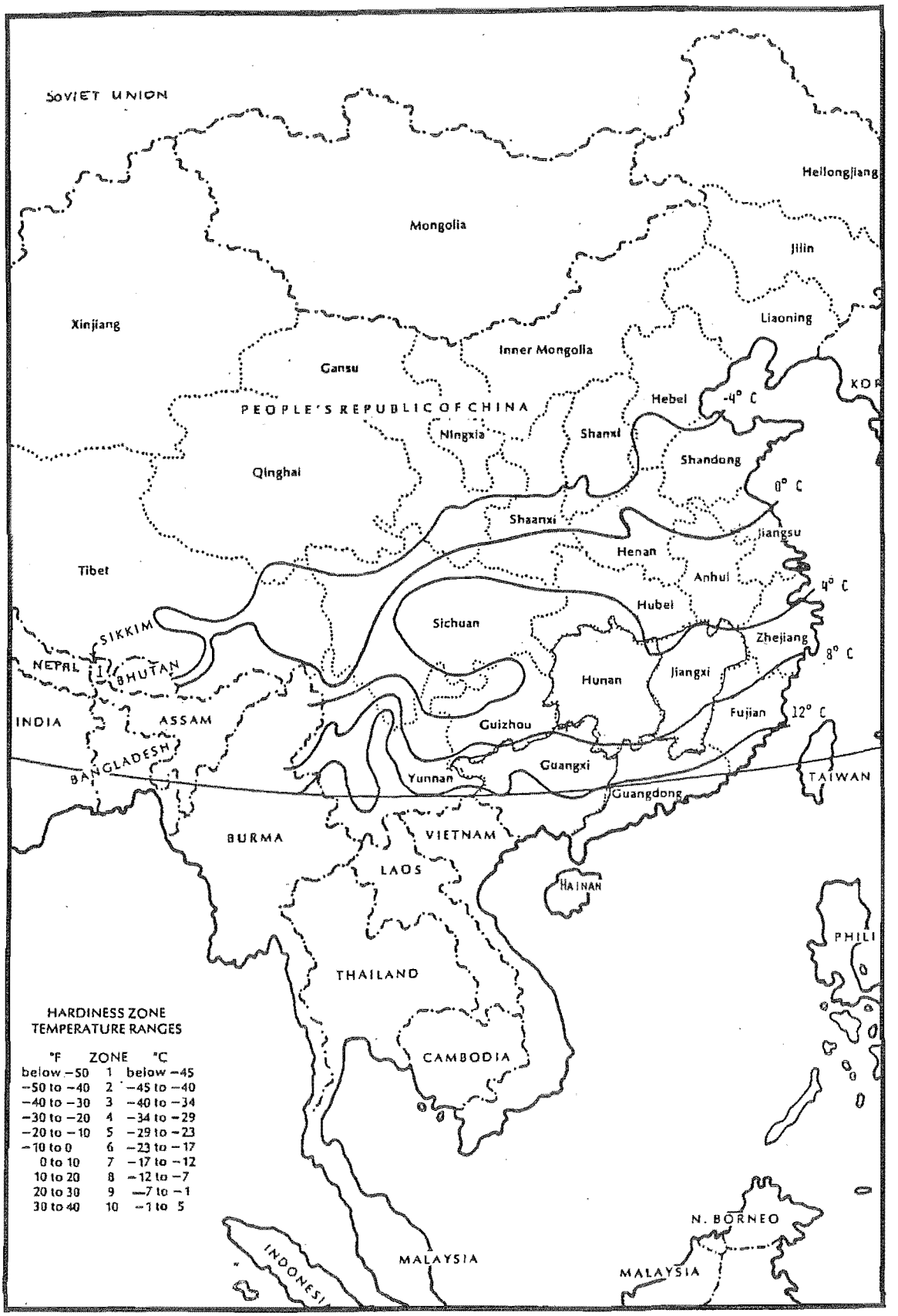
Footnotes :
1. Sex unknown, plant not yet fruited.
2. These genotypes of *A. chinensis* var. *chinensis* have alternative names :
3/6/7a = 460.4
3/6/9a = 460.9
Latter designations are used in results tables.

Abbreviations :
K = Kumeu Research Orchard, D.S.I.R., Fruit and Trees
T.P. = Te Puke Research Orchard, D.S.I.R., Fruit and Trees

Table 3.2 **Genotypes of *A. chinensis* var. *chinensis***

Selection	Province and District of Origin	Genotypes chosen		
CN14	Guangxi Guilin street stall	F4I5	G4H1	G4H5
CN15	Guangxi Longsheng	G4B3	G4H4	G4B5
CN12	Hunan Linyang county North of Changshu	G2A4	F4B5	G3A5
CN07	Hunan Lingang county	G2D6	G2E6	G2F3
CN17	Jiangxi Wanti district Meiling	G3C3	G3C2	G3C1
CN17	Jiangxi Lushan mountain	G4D5	G4D2	G4D3

Figure 3.1 : Map of Eastern Asia [after Krüssmann 1984]



Quantitative data are presented as ranges following standard taxonomic treatments (e.g. Liang 1984) and arithmetic means of measurement variables used for cluster analysis are presented in Appendix 3.1.

3.2.4 Bud photography

Winter shoots were photographed using electronic flash lighting with a 35 mm SLR camera, equipped with a macro-lenses designed to produce a 1:1 magnification of the film. A pale amber filter (81B type) was also used. Images were recorded on Fuji 50 (daylight) 35 mm colour slide film, processed E.6.

Bud dissections buds were photographed with the aid of a stereoscopic microscope (Wild Photomakroscop M400), equipped with a fibre optics lighting unit (Schott KL 1500) with a colour temperature of 3200 K. Images were recorded on Kodak Ektachrome 160 (tungsten) 35 mm colour slide film.

3.2.5 Selection of variables

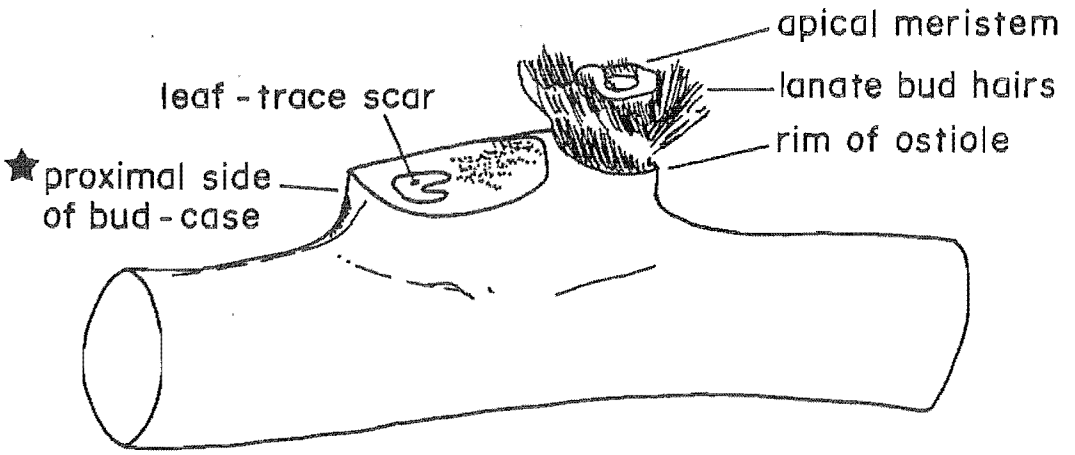
Twenty three variables (characters) were derived from winter shoots, of these 6 were ratio variables and 1 was chosen subjectively (stem colour). The complete matrix of species x variables (32 taxa x 23 variables) is presented in Appendix 3.1. The data set comprised 32 taxa x 23 variables x 10 replicates obtained from 1 or 2 selected plants, representative of the variation contained in the D.S.I.R. Kiwifruit germplasm collection.

Descriptive statistics for cluster analysis were generated using S.A.S. univariate procedures for personal computers.

Lenticel densities and hair base densities were obtained using a stereoscopic microscope.

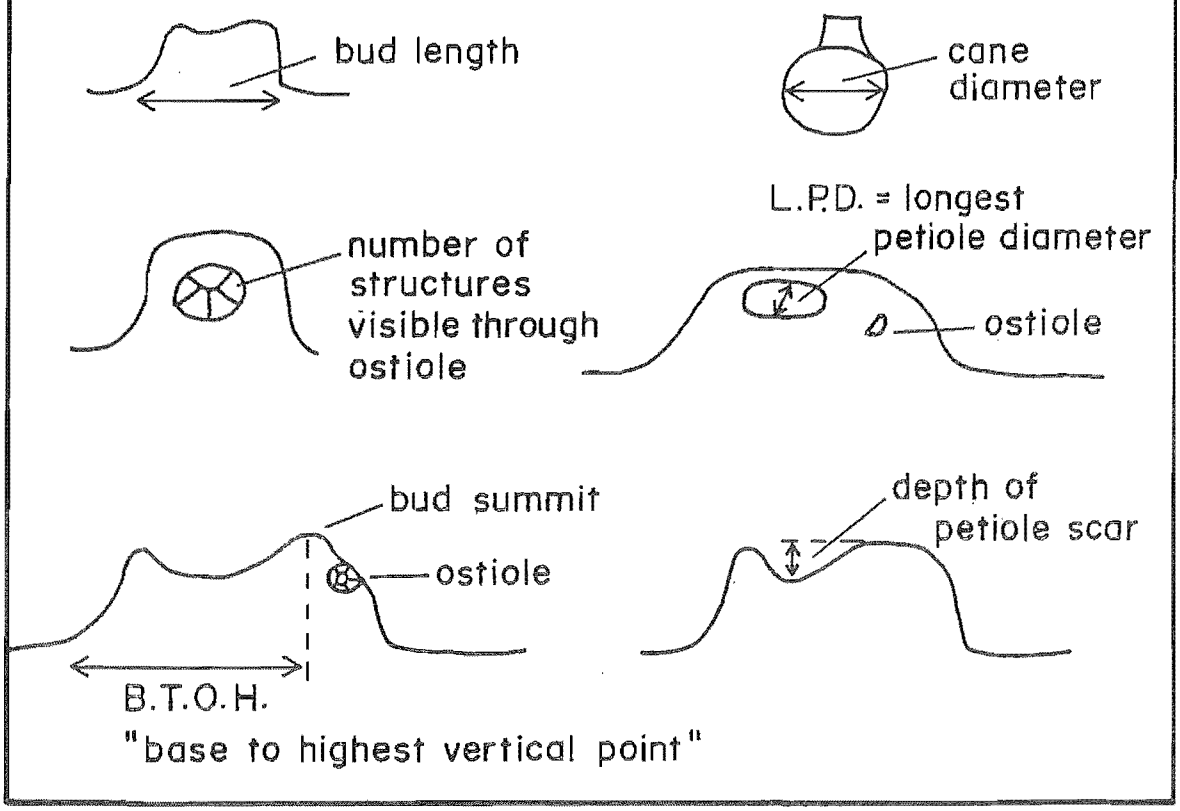
Cluster analysis of winter shoot characters was performed as described in the previous chapter. Discriminant analysis is explained in Section 3.3.3.

Figure 3·2: External parts of an *A. deliciosa* bud soon after bud - burst



★ after Zhang and Thorp (1986)

Figure 3·3: Selected bud measurements (mm)



3.3 RESULTS

3.3.1 Descriptions of winter shoots in some *Actinidia*

This section summarises the main trends in the descriptive data (Tables 3.2-3.6).

3.3.1.1 *Stem surface*

The colour of 1 year canes is mainly chestnut-brown in plants of the *Leiocarpae*, increasingly red-purple in the *Maculatae* and *Strigosae*, and is basically chocolate-brown to green-ochre in the *Stellatae* (Table 3.3, Figure 3.4.1).

Cane texture is smooth and glossy in the *Leiocarpae* and *Maculatae* (Plates 3.1, 3.2) with the bark assuming a matt to asperous texture in the *Stellatae.* (Plates 3.3, 3.4). The *Leiocarpae* and *Maculatae* examined are glabrous except for *A. rufa.* Other *Actinidia* have red-purple to orange-brown hairs of a hispid type. Hairs of the *Strigosae* are long and entire, whereas, those of the *Stellatae* occur mostly as stubble-like remains of hair bases, with canes of variety *chlorocarpa* being the notable exception in having entire hairs at maturity (Plate 3.3)..

Lenticels in 1 year canes usually have orange-brown centres with cream to fawn edges, frequently becoming more whitish in the *Stellatae* (Plate 3.4). Lenticels seen on winter canes are not as coloured as those of actively growing summer shoots (see Chapter Two). Lenticels are ovoid and elongate in all but the *Stellatae*, where they are shorter and more spherical in form. The longest lenticels are 1-2 mm in most *Actinidia*, but they may be 2-3 times this length, (e.g. *A. latifolia*, *A. chinensis*). The degree of lenticel protuberance can aid in plant identification. Most *Leiocarpae*, *Maculatae* and *Strigosae* have slightly raised lenticels, but some taxa such as *A. polygama*, *A. chrysantha* and *A. indochinensis* can almost be distinguished by their protuberant lenticels alone (Plate 3.2 E,F). Lenticel density decreases markedly from the *Leiocarpae* to the *Stellatae*, with *A. rufa* and *A. callosa* var. *henryi* being the exceptions (Figure 3.4.2, Plate 3.2).

3.3.1.2 *Bud form*

Buds of the *Leiocarpae* are narrower, more triangular and lower in height than those of other *Actinidia* (Plate 3.1). The bud-case is usually more rounded than in other taxa (Tables 3.4 page 2, 3.5, Plates 3.1-3.4, Figures 3.4.3-3.4.7). In winter shoots of *A. arguta* var. *cordifolia*, the upper surface of the bud-case has two cats-ear-like projections arising from the proximal summit of the petiole scar,

(Plate 3.1 E;F). The average diameter of the petiole scar, when measured from the top of the bud-case, distinguishes the *Stellatae* from other sections of the genus (Figure 3.4.13). Some cultivars of *A. deliciosa* have small petiole scars, (e.g. 'Allison', 'Matua'), whereas others such as 'Gracie', 'Jones', 'Monty', 1 Elmwood' have large petiole scars. The shape of the vascular bundle on the petiole scar is a characteristic of many taxa (see also Gao 1988, Metcalfe and Chalk 1950).

Winter buds of the *Maculatae* are square to triangular in shape (Plate 3.2). The *Stellatae* have large protuberant buds triangular to rectangular in form. Bud shape can be quantified using the bud-length to bud-height ratio (Figure 3.4.14), the B.T.O.H. figure (base to highest vertical point, see Figure 3.4.7) and also in terms of its components (Figures 3.4.3-3.4.5). The relative slope of distal and proximal sides of the bud-case (see in profile) enables some plants to be identified to the cultivar level, as verified by Zhang and Thorp (1986).

Variations in the shape of the proximal, or petiole, side of the bud are subtle in comparison with those of the distal side. The proximal side (Figure 3.2) is gradually sloping in the *Leiocarpae* (Plate 3.1), becoming abrupt toward the petiole and concave near the cane in the *Maculatae* and *Strigosae*. Buds of the *Stellatae* have a slope which increases gradually over a greater proportion of the proximal side (Plates 3.3, 3.4).

The length of the distal face of the bud when measured from the edge of the bud scar to the cane is short to medium in most taxa, but medium to long in the *Stellatae*.

Winter buds of the *Leiocarpae* are convex from the petiole above the ostiole are stepped in profile toward the ostiole and gently concave below. Bud-cases of the *Maculatae* and *Strigosae* are more variable in the form of their distal sides. Buds of the *Stellatae* are mostly convex from the petiole to the ostiole, with their profile toward the cane becoming variously straight to concave. The distal slope of the bud face is diverse in Section *Stellatae*. In *A. chinensis* the distal bud profile is short and abrupt, becoming basally concave, but in buds of *A. deliciosa* (Plates 3.3, 3.4) the distal side may change from straight to concave, (e.g. 'Abbott', 'Allison'), or be gently concave as in cultivars 'Bruno', 'Gracie' and Matua. The distal profile may be very long as in 'Jones' or distinctively tall and straight on top, becoming concave below, as in cv. Elmwood (Plate 3.4 E,F) (see also Zhang and Thorp 1986).

3.3.1.3 *Bud emergence*

The *Actinidia* surveyed have characteristic bud shapes, but are equally distinctive in their bud emergence characters. Dissection of winter buds shows that

most taxa have bud-cases concealing a single shoot. *Actinidia callosa* var. *henryi* is the only plant studied where each bud bears three potentially productive shoots, each with its own set of scales. The central shoot is larger and bears a greater number of protective structures, whereas the other two buds are smaller in size and axillary to the first.

Bud-case nomenclature is adapted from Zhang and Thorp (1986), where distal and proximal sides of the bud are defined with reference to the "petiole side" of the bud (Figure 3.2).

The 'ostiole' is the small opening through which the shoot emerges in the spring (Figure 3.2). The diameter of the ostiole is minute ($\leqslant$ 2 mm) in the *Leiocarpae* (Plate 3.2, ~ 2-4 mm), *Strigosae* and *Stellatae* in part (*A. latifolia*, *A. eriantha*). *A. chinensis* (Plate 3.7) and *A. latifolia* (Plate 3.3) have very large ostioles (5-8 mm), whereas *A. deliciosa* has small ostioles like those of the *Leiocarpae* (Plate 3.1). *A. rufa* has much larger ostioles than other *Leiocarpae*, to which it is allegedly related (Liang 1984). The ratio of ostiole size relative to the width of the bud (Figure 3.4.14) provides a further measure of ostiole size and produces three groupings of taxa:

1. *arguta-kolomikta.*
2. *deliciosa* cultivars.
3. *Maculatae-Strigosae-Stellatae* in part.

The ostiole is positioned on the mid to upper third of the petiole side of the bud case, in the *Leiocarpae*, *Maculatae* and *Strigosae*. The *Stellatae* have large ostioles which almost touch the base of the petiole (e.g. *A. latifolia* and *A. chinensis*); alternatively, ostioles may occur as minute structures which are positioned high on the distal side of the bud, as in *A. deliciosa*.

Most *Leiocarpae* have $\leqslant$ 1.0 "shoot structure" visible through the ostiole. Plants of series *Solidae* have up to 5 "visible shoot structures". Buds of Sections *Strigosae* and *Stellatae*, excluding *A. deliciosa*, have twice as many shoot structures visible through the exterior of ostiole (Figure 3.4.12). Buds of *A. chinensis* have the highest number of shoot structures visible from the outside of the ostiole.

Both the *Leiocarpae* and *Stellatae* have up to 2 mm of "shoot structures" protruding above the outermost surface of the ostiole. Winter shoots of the Maculatae and *A. latifolia* and *A. eriantha* of the *Stellatae* can extend 0.5 cm above the ostiole (Figure 3.4.11).

It is apparent that some of the groupings derived from examination of bud emergence characters disagree with the taxonomic groupings (sections) as proposed by Liang (1984).

Table 3.3 Cane surfaces of some *Actinidia*

Taxon	Stem colour	Stem texture gloss	Stem hair quality colour	Stem hair extent length	Stem hair-base density (cm^{-2})
A. arguta var. *arguta*	chestnut-brown to fawn-ochre beneath	smooth polished, glossy	N.A.	N.A.	0.00
A. arguta var. *purpurea*	greenish chestnut-brown to fawn-ochre beneath	smooth polished, glossy	N.A.	N.A.	0.00
A.arguta var. *giraldii*	chestnut-brown more ochre beneath	smooth polished, glossy	N.A.	N.A.	0.00
A. arguta var. *cordifolia*	chestnut brown to fawn-ochre beneath	smooth polished, glossy	N.A.	N.A.	0.00
A. rufa	variable ochre-fawn to green beneath, darker brown above	semi-smooth bumpy lenticels matt	minute, hispid orange-brown	many hair bases much fine stubble on young shoots	200.00-1500.00
A. melanandra var. *melanandra*	mid to chestnut-brown, fawn-ochre beneath	smooth polished, glossy	N.A.	N.A.	0.00
A. kolomikta	red-purple to chestnut-brown	smooth polished, glossy	N.A.	N.A.	0.00
A. polygama 3/12/11*	variable: red-purple overlain by pale fawn to ochre	smooth bumpy lenticels polished, glossy	N.A.	N.A.	0.00
A. valvata var. *valvata*	fawn-brown to greyish	smooth bumpy lenticels matt	N.A.	N.A.	0.00
A. callosa var. *henryi*	orange-brown with green hue to fawn-ochre beneath	smooth polished, glossy	N.A.	N.A.	0.00

Table 3.3 continued next page

Table 3.3. continued

Taxon	Stem colour	Stem texture gloss	Stem hair quality colour	Stem hair extent length	Stem hair-base density (cm^{-2})
A. chrysantha	chestnut-brown with slight red-purple hue	smooth bumpy lenticels semi-glossy to glossy	N.A.	N.A.	0.00
A. indochinensis 36/3/11b*	dark red-purple to black	smooth semi-glossy to glossy	N.A.	N.A.	0.00
A. melliana	ochre to red-brown hairs give red hue to stem	bristly, matt	hirsute red to red-purple	entire wide-spread 2-3 mm	45.00-150.00
A. hemsleyana var. *hemsleyana*	chestnut-brown to ochre beneath	felty tomentose, matt	tomentose orange-brown	hair-bases common, many entire hairs near bud-base	20.00-1000.00
A. latifolia	red-purple to chocolate-brown	smooth glabrous, glossy	N.A.	N.A.	0.00
A. eriantha	incanescent whitish green	soft, felty, tomentose, matt	tomentose whitish	hairs extremely dense, all entire, no bark visible	1290.00-3740.00
A. chinensis var. *chinensis* 3/6/14b*	chocolate-brown above, fawn-ochre beneath	smooth, semi-glossy	scarceley visible basic-ally hairless	mostly hair-bases, some stubble near bud-cases	1.00-30.00
A. deliciosa var. *deliciosa* 'Hayward'	Greenish ochre to brown	rough, asperous matt	hispid orange-brown	mostly hair-bases and stubble, entire rare	48.00-160.00
" " 'Bruno'	Chocolate-brown with slight red hue	rough, asperous matt	hispid orange-brown	mostly hair-bases, some stubble near bud cases	100.00-1200.00
" " 'Abbott'	Greenish ochre to brown	rough, asperous matt	hispid orange-brown	mostly hair-bases, and stubble, some entire hairs on bud-case	40.00-160.00

Table 3.3 continued next page

Table 3.3 continued

Taxon	Stem colour	Stem texture gloss	Stem-hair quality colour	Stem-hair extent length	Stem hair-base density (cm^{-2})
A. deliciosa var. *deliciosa* 'Gracie'	greenish ochre to brown	rough, asperous matt	hispid orange-brown	mostly obvious stubble hairs entire near bud-case	32.00-100.00
" " 'Greensill'	greenish ochre to dark brown	rough, asperous matt	hispid orange-brown	mostly hair bases and stubble, hairs entire on bud	60.00-200.00
" " 'Allison'	greenish ochre to brown	rough, asperous matt	Hispid orange-brown	mostly hair bases and stubble, hair entire on bud-case	88.00-164.00
" " 'Matua'	greenish ochre to brown	rough, asperous matt	hispid orange-brown	mostly hair bases and stubble, some entire hairs on bud-case	15.00-480.00
" " 'Jones'	greenish ochre to brown	rough, asperous matt	hispid orange-brown	hairs mostly stubble hairs entire near bud-case	35.00-104.00
" " 'Monty'	greenish ochre to brown	rough, asperous matt	hispid orange-brown	mostly hair bases stubble near bud-case	80.00-200.00
" " 'Elmwood'	greenish ochre to brown	rough, asperous matt	hispid orange-brown	hairs mostly bases and stubble, entire near bud-case	12.00-320.00

Table 3.3 continued next page

Table 3.3 continued

Taxon	Stem colour	Stem texture gloss	Stem hair quality colour	Stem hair extent length	Stem hair-base density (cm^{-2})
A. deliciosa var. *chlorocarpa*	green to brown	rough, asperous matt	hispid to setose orange-brown	hairs mainly entire some stubble	100.00-180.00

Footnotes :
(1) N.A. = non-applicable as plant glabrous
(2) Hairs may be: (i) entire $\leqslant$ 1.0 mm long
(ii) stubble + base $\leqslant$ 0.2 mm long
(iii) hair base only
(3) Beneath = along the underside of the cane
(4) Stem hair base density and stem hair extent and length determined with stereo-microscope
* Numbers are different genotypes for all tables in this chapter

Table 3.4 Form of Lenticels on Some *Actinidia* Canes

Taxon	Lenticel colour	Lenticel shape	Lenticel protuberance (mm)	Length of longest lenticel (mm)	Lenticel density on cane (cm^{-2})
A. arguta var. *arguta*	variable: cream-white to orange-brown	mostly ovoid and elongate	slightly raised	1.50 - 2.00	36.00 - 64.00
A. arguta var. *purpurea*	consistent orange-brown	mostly ovoid and elongate	slightly raised	1.80 - 3.50	15.00 - 52.00
A. arguta var. *giraldi*	variable: younger orange-brown older cream-white	mostly ovoid and elongate	slightly raised	0.50 - 2.00	20.00 - 48.00
A. arguta var. *cordifolia*	consistent: orange-brown	mostly ovoid and elongate	slightly raised	1.20 - 2.00	20.00 - 40.00
A. rufa	younger, orange-brown to white, older becoming cream-whitish	mostly elongate some ovoid	protuberant	2.00 - 5.00	6.00 - 12.00
A. melanandra var. *melanandra*	younger, orange-brown older, whitish	mostly spherical and ovoid	raised	0.60 - 1.50	24.00 - 44.00
A. kolomikta	orange-brown centres fawn-brown edges	mostly ovoid and spherical	raised	0.60 - 1.20	9.00 - 32.00
A. polygama 3/12/11	orange-brown centres cream-fawn edges	mostly elongate few ovoid and spherical	protuberant	3.00 - 6.00	4.00 - 15.00
A. valvata	younger, cream-white older ruptured with dark chestnut-brown centres	mostly spherical and ovoid	raised	1.20 - 4.00	8.00 - 20.00
A. callosa var. *henryi*	orange-brown to grey centres, cream-white edges	mostly spherical and ovoid	slightly raised	0.60 - 1.80	24.00 - 86.00

Table 3.4 continued next page

Table 3.4. continued

Taxon	Lenticel colour	Lenticel shape	Lenticel protuberance (mm)	Length of longest lenticel (mm)	Lenticel density on cane (cm^{-2})
A. chrysantha	orange-brown centres cream on old canes	mostly ovoid and elongate	raised to protuberant	1.20 - 3.00	8.00 - 24.00
A. indochinensis 36/3/11b	younger cream-yellow, older orange-brown	mostly ovoid and elongate	raised to protuberant	2.00 - 4.50	8.00 - 20.00
A. melliana	fawn-grey centres cream-white edges	mostly ovoid and elongate	raised	1.20 - 2.00	16.00 - 24.00
A. hemsleyana var. *hemsleyana*	variable: orange-brown centres, fawn edges	mostly spherical and ovoid	raised	0.80 - 1.50	4.00 - 20.00
A. latifolia	orange-brown centres cream-white edges	mostly elongate fewer ovoid	raised	3.00 - 5.00	4.00 - 24.00
A. eriantha	normally invisible, if hairs removed lenticels orange	mostly elongate	inconspicuous due to stem pubescence	0.40 - 2.20	12.00 - 40.00
A. chinensis var. *chinensis* 3/6/14b	pale orange-brown centres cream-white edges	mostly spherical and ovoid	raised to protuberant	3.00 - 7.00	4.00 - 24.00
A. deliciosa var. *deliciosa* 'Hayward'	pale orange-brown centres, cream-white edges	spherical and ovoid	raised	0.60 - 3.00	6.00 - 20.00
" " 'Bruno'	pale orange-brown centres, cream-white edges	spherical and ovoid	raised to inconspicuous	1.20 - 2.00	0.60 - 2.30
" " 'Abbott'	orange-brown centres, cream-white edges	spherical and ovoid	raised to inconspicuous	0.20 - 1.50	8.00 - 20.00

Table 3.4. continued

Taxon	Lenticel colour	Lenticel shape	Lenticel protuberance (mm)	Length of longest lenticel (mm)	Lenticel density on cane (cm^{-2})
A.deliciosa var. *deliciosa* 'Gracie'	pale orange-brown centres, cream-white edges	spherical and ovoid	raised	1.80 - 3.00	6.00 - 20.00
" " 'Greensill'	pale orange-brown centres, cream-white edges	spherical and ovoid	raised	1.10 - 5.00	4.00 - 16.00
" " 'Allison'	pale orange-brown centres, cream-white edges	spherical and ovoid	raised to conspicuous	0.60 - 1.80	9.00 - 16.00
" " 'Matua'	orange-brown centres, cream-fawn edges	spherical and ovoid	raised	0.70 - 5.00	4.00 - 16.00
" " 'Jones'	orange-brown centres, cream-white edges	spherical and ovoid	raised	0.60 - 2.60	8.00 - 12.00
" " 'Monty'	pale orange-brown centres, cream-white edges	spherical and ovoid	raised to inconspicuous	0.60 - 2.00	8.00 - 20.00
" " 'Elmwood'	minute, pale orange-brown centres, cream-white edges	spherical and ovoid	raised to inconspicuous	1.80 - 4.00	13.00 - 20.00

Table 3.4 continued next page

Table 3.4. continued

Taxon	Lenticel colour	Lenticel shape	Lenticel protuberance (mm)	Length of longest lenticel (mm)	Lenticel density on cane (cm^{-2})
A. deliciosa var. *chlorocarpa*	orange-brown centres, fawn-cream edges	spherical and ovoid	raised	1.00 - 2.00	15.00 - 60.00

Footnotes : Lenticel shape Categories :

1 - 2:1 = spherical
2 - 3:1 = ovoid
$\geqslant$ 3-4:1 = elongate

Table 3.5(a) **Bud shape in some *Actinidia***

Taxon	Bud-case shape (profile view)	Bud-case length (mm)	Bud-case height (mm)	Bud-case length : height ratio
A. arguta var. *arguta*	long triangular uneven	7.00 - 13.00	3.00 - 4.00	1.75 - 4.33
A. arguta var. *purpurea*	triangular pointed	10.00 - 12.00	3.00 - 4.00	2.00 - 4.00
A. arguta var. *giraldii*	triangular to rectangular	10.00 - 14.00	2.50 - 4.50	2.66 - 4.00
A. arguta var. *cordifolia*	long triangular uneven	10.00 - 15.00	4.00 - 5.00	2.50 - 3.75
A. rufa	rectangular to triangular	8.00 - 13.00	6.00 - 9.00	1.30 - 3.00
A. melanandra var. *melanandra*	triangular to square	5.50 - 10.00	3.00 - 5.00	1.63 - 2.50
A. kolomikta	triangular to rectangular	6.00 - 9.00	3.00 - 5.00	1.55 - 2.33
A. polygama 3/12/11	triangular to rectangular	7.00 - 10.00	2.00 - 6.00	1.60 - 4.00
A. valvata	square to triangular	8.00 - 13.00	3.00 - 5.00	1.60 - 3.66
A. callosa var. *henryi*	square	5.00 - 8.00	4.00 - 6.00	0.93 - 1.75
A. chrysantha	triangular to square	7.00 - 10.00	4.00 - 7.00	1.14 - 2.00
A. indochinensis 36/3/11b	triangular symmetrical	8.00 - 11.00	2.10 - 4.00	2.38 - 4.00
A. melliana	triangular to square	7.00 - 9.00	4.50 - 6.00	1.33 - 2.00

Table 3.5 continued next page

Table 3.5(a) Continued

Taxon	Bud-case shape (profile view)	Bud-case length (mm)	Bud-case height (mm)	Bud-case length : height ratio
A. hemsleyana var. *hemsleyana*	rectangular to square	12.00 - 14.00	4.00 - 6.00	2.00 - 3.25
A. latifolia	triangular to square	9.00 - 13.00	5.00 - 8.00	1.12 - 2.33
A. eriantha	triangular to square	10.00 - 15.00	6.00 - 8.00	1.25 - 2.50
A. chinensis var. *chinensis* 3/6/14b	triangular to square	8.00 - 13.00	5.50 - 9.00	0.88 - 3.00
A. deliciosa var. *deliciosa*	rectangular to triangular	12.00 - 20.00	6.00 - 9.00	1.50 - 2.57
" " 'Hayward'				
" " 'Bruno'	rectangular to triangular	12.00 - 20.00	7.00 - 10.00	1.62 - 2.85
" " 'Abbott'	rectangular to triangular	13.00 - 20.00	5.00 - 9.00	1.62 - 3.60
A. deliciosa var. *deliciosa*	rectangular symmetrical	15.00 - 22.00	6.00 - 8.00	1.87 - 3.33
" " 'Gracie'				
" " 'Greensill'	rectangular to triangular	12.00 - 22.00	5.00 - 9.00	1.60 - 4.00
" " 'Allison'	rectangular to triangular	15.00 - 20.00	5.00 - 8.00	2.25 - 4.00
" " 'Matua'	rectangular to triangular variable	12.00 - 16.00	5.00 - 8.00	1.71 - 3.75
" " 'Jones'	rectangular symmetrical	15.00 - 25.00	5.00 - 8.00	2.12 - 4.16
" " 'Monty'	rectangular triangular	12.00 - 22.00	4.00 - 9.00	1.41 - 5.00

Table 3.5(a) Continued

Taxon	Bud-case shape (profile view)	Bud-case length (mm)	Bud-case height (mm)	Bud-case length : height ratio
A. deliciosa var. *deliciosa*				
" " 'Elmwood'	high, square to rectangular	15.00 - 20.00	8.00 - 11.00	1.50 - 2.50
A. deliciosa var. *chlorocarpa*	rectangular to triangular symmetrical	10.00 - 13.00	6.00 - 8.00	1.25 - 2.40

Table 3.5 continued next page

Table 3.5(b)

Taxon	Bud-case width (mm)	B.T.O.H.distance from proximal side to bud summit (mm)	Length : proximal slope of bud-case	Length : distal slope of the bud-case
A. arguta var. *arguta*	5.00 - 6.00	3.00 - 6.00	very short : gradually concave	medium : concave, stepped near ostiole, gently concave below
A. arguta var. *purpurea*	5.50 - 7.00	4.00 - 7.00	very short : gradually concave	short to medium : concave, stepped near ostiole : gently concave below
A. arguta var. *giraldii*	4.00 - 7.00	0.00 - 1.00	short : slightly concave almost upright	long : convex top, middle concave stepped, short straight concave to base
A. arguta var. *cordifolia*	6.00 - 7.50	0.00 - 1.00	short : slightly concave almost upright	long : convex top, middle concave stepped, short straight concave to base
A. rufa	5.00 - 7.50	4.00 - 8.00	short : gently concave below variable at times abrupt	short : abrupt to concave near base
A. melanandra var. *melanandra*	4.50 - 7.00	3.00 - 5.00	short : abrupt near petiole scarcely concave near base	medium : shortly concave, stepped near ostiole, gently concave below
A. kolomikta	2.20 - 6.00	3.00 - 4.50	short : abrupt near petiole, gently concave below	short to medium : gently concave to stepped near ostiole, gently concave

Table 3.5 continued next page

Table 3.5(b) continued

Taxon	Bud-case width (mm)	B.T.O.H.distance from proximal side to bud summit (mm)	Length : proximal slope of bud-case	Length : distal slope of the bud-case
A. polygama 3/12/11	4.50 - 6.50	2.00 - 6.00	short : abrupt near petiole, gently concave below	medium : convex to ostiole, concave below
A. valvata	4.30 - 9.00	4.00 - 6.50	short : abrupt, scarcely concave near base	medium : convex to ostiole gently concave below
A. callosa var. *henryi*	4.00 - 7.00	2.00 - 4.20	short to medium, abrupt to scarcely concave near base	short : abrupt from ostiole to base
A. chrysantha	4.00 - 6.00	3.00 - 6.50	medium : abrupt scarcely concave near base	medium : gently concave, stepped near ostiole, gently concave below
A. indochinensis 36/3/11a	4.00 - 5.00	5.00 - 7.00	short : abrupt to concave near base	short : gently convex to bud, concave below
A. melliana	4.50 - 6.50	5.00 - 7.00	short : abrupt to gently concave near base	short to medium : convex to straight toward base
A. hemsleyana var. *hemsleyana*	5.50 - 7.00	2.00 - 3.50	short to medium : gently concave to base	short to medium : convex near ostiole, gently concave below

Table 3.5 continued next page

Table 3.5(b) continued

Taxon	Bud-case width (mm)	B.T.O.H.distance from proximal side to bud summit (mm)	Length : proximal slope of bud-case	Length : distal slope of the bud-case
A. latifolia	6.50 - 9.00	4.00 - 8.00	short : shortly abrupt to gently concave near base	very short : slightly straight to convex near base
A. eriantha	5.50 - 11.00	4.00 - 8.00	short : shortly abrupt to gently concave near base	short to very short : abrupt to gently concave near base
A. chinensis var. *chinensis* 3/6/14b	6.00 - 8.00	4.00 - 7.00	short : abrupt to gently concave near base	short : abrupt near base
A. deliciosa var. *deliciosa*				
" " 'Hayward'	6.00 - 10.00	8.20 - 10.20	short : abrupt to gently concave near base	medium : convex to ostiole straight to concave below
" " 'Bruno'	6.50 - 8.00	4.00 - 12.00	short : shortly abrupt to gently concave below	medium to long : convex to ostiole, straight to concave belows
" " 'Abbott'	6.00 - 8.00	8.50 - 12.00	short : gently concave gradual	medium : convex to ostiole gently concave below

Table 3.5 continued next page

Table 3.5(b) continued

Taxon	Bud-case width (mm)	B.T.O.H.distance from proximal side to bud summit (mm)	Length : proximal slope of bud-case	Length : distal slope of the bud-case
A. deliciosa var. *deliciosa*				
" " 'Gracie'	8.00 - 9.00	9.80 - 13.00	short : gently concave gradual gradual	medium : convex to ostiole, straight to concave below
" " 'Greensill'	7.00 - 10.00	7.50 - 13.00	medium : shortly abrupt to gently concave below	medium : convex to ostiole, straight to convex near base
" " 'Allison'	6.00 - 8.00	5.00 - 12.00	short : gently concave gradual	medium : convex to ostiole, gently concave below
" " 'Matua'	6.00 - 8.00	2.00 - 10.50	short : shortly abrupt to gently concave near base	medium: convex to ostiole, straight to concave below
" " 'Jones'	6.00 - 10.00	7.20 - 16.00	short to medium : gently concave gradual	medium to long : convex to ostiole, gently concave below

Table 3.5 continued next page

Table 3.5(b) continued

Taxon	Bud-case width (mm)	B.T.O.H.distance from proximal side to bud summit (mm)	Length : proximal slope of bud-case	Length : distal slope of the bud-case
A. deliciosa var. *deliciosa*				
" " 'Monty'	1.00 - 10.00	2.00 - 12.00	medium : shortly straight to gently concave below	tall : convex to ostiole gently concave below
" " 'Elmwood'	8.00 - 11.00	6.50 - 14.00	short : abrupt scarcely concave at base	tall : convex to ostiole straight below concave near base
A. deliciosa var. *chlorocarpa*	6.20 - 9.00	6.00 - 10.00	short : slightly concave almost upright	medium to long : convex to ostiole, gently concave below

Footnotes:
(1) "length" is relative measure of distance from petiole base to base of bud-case.
(2) Profiles of distal and proximal slopes are described from the petiole base toward the ostiole and thence toward the base of the bud case.
(3) Distal and proximal (after Zhang and Thorpe 1986) are used with reference to petiole side of the bud-case.

Table 3.6 Bud emergence characters of some *Actinidia*

Taxon	Number of shoots	ostiole width (mm)	Ostiole : position on distal side distance from petiole base	Number of bud structures visible through ostiole	Height of visible bud structures (mm)
A. arguta var. *arguta*	One	0.00 - 0.25	mid-distal, at base of hollow. 2 mm from petiole base	1.00	0.00
A. arguta var. *purpurea*	One	0.25 - 1.00	mid to upper $\frac{1}{3}$ distal, base of hollow. 2 mm from petiole base	1.00	0.20 - 0.50
A. arguta var. *giraldii*	One	0.10 - 0.50	mid to upper $\frac{1}{3}$ distal on stepped rise 2 mm from petiole base	0.00 - 1.00	0.10 - 1.00
A. arguta var. *cordifolia*		1.00 - 1.50	mid to upper $\frac{1}{3}$ distal on stepped rise 2 mm from petiole base	0.00 - 1.00	0.00 - 1.00
A. rufa	One	2.00 - 4.00	occupies mid to upper $\frac{1}{3}$ distal touching petiole base	2.00 - 7.00	1.00 - 2.50
A. melanandra var. *melanandra*	One	0.25 - 6.00	mid-distal on stepped rise 2 mm from petiole base	0.00 - 1.00	0.10 - 0.50
A. kolomikta	One	0.25 - 1.50	mid-distal in base of hollow 1-2 mm from petiole base	1.00 - 2.00	0.25 - 0.50
A. polygama 3/12/11*	One	1.00 - 2.00	mid to upper $\frac{1}{3}$ distal 2 mm from petiole base	1.00 - 5.00	0.25 - 1.50
A. valvata	One	1.50 - 2.50	upper $\frac{1}{4}$ distal 1 mm from petiole base	3.00 - 4.00	0.25 - 1.20

Table 3.6 continued next page

Table 3.6. continued

Taxon	Number of shoots	ostiole width (mm)	Ostiole : position on distal side distance from petiole base	Number of bud structures visible through ostiole	Height of visible bud structures (mm)
A. callosa var. *henryi*	Three	3.00 - 7.00	upper $\frac{1}{2}$ distal to touching petiole base	5.00 - 12.00	2.00 - 3.50
A. chrysantha	One	2.50 - 4.00	occupies mid to upper $\frac{1}{3}$ distal side 1 mm from petiole base	3.00 - 8.00	1.00 - 2.00
A. indochinensis 36/3/11b	One	3.50 - 4.00	upper $\frac{1}{3}$ to $\frac{1}{2}$ distal 1 mm from petiole base	5.00 - 8.00	1.00 - 2.00
A. melliana	One	2.00 - 5.00	mid to upper $\frac{1}{3}$ distal touching petiole base	2.00 - 5.00	1.50 - 2.50
A. hemsleyana var. *hemsleyana*	One	3.00 - 4.50	upper $\frac{1}{3}$ distal touching petiole base	3.00 - 6.00	0.50 - 1.50
A. latifolia	One	5.00 - 8.00	mid to upper $\frac{1}{3}$ distal touching petiole base	4.00 - 9.00	1.50 - 4.50
A. eriantha	One	4.50 - 7.00	upper $\frac{1}{2}$ distal to touching petiole base	5.00 - 7.00	1.50 - 3.00
A. chinensis var. *chinensis* 3/6/14b	One	5.50 - 8.00	upper $\frac{1}{2}$ distal to touching petiole base	7.00 - 12.00	2.50 - 4.50
A. deliciosa var. *deliciosa*	One	1.00 - 4.00	top distal flattish area, upper 1/4 to 1/5 distal	1.00 - 5.00	0.25 - 1.00
" " 'Hayward'					
" " 'Bruno'	One	0.50 - 2.50	top distal, gently curved upper 1/5 to 1/6 distal 1 mm from petiole base	1.00 - 2.00	0.00 - 1.00

Table 3.6 continued next page

Table 3.6. continued

Taxon	Number of shoots	ostiole width (mm)	Ostiole : position on distal side distance from petiole base	Number of bud structures visible through ostiole	Height of visible bud structures (mm)
A. deliciosa var. *deliciosa*					
" " 'Abbott'	One	1.00 - 2.00	top distal, flattish area, upper 1/4 to 1/5 distal 1 mm from petiole base	1.00 - 3.00	0.25 - 1.50
" " 'Gracie'	One	1.00 - 2.00	top distal, flattish area upper 1/4 to 1/5 distal touching petiole base	1.00 - 3.00	0.00 - 0.25
" " 'Greensill'	One	0.50 - 2.00	top distal, flattish area upper 1/4 to 1/5 distal 1 mm from petiole base	1.00 - 2.00	0.25 - 1.00
" " 'Allison'	One	1.00 - 2.50	top distal, flattish area upper 1/4 to 1/5 distal touching petiole base	1.00 - 4.00	0.25 - 1.00
" " 'Matua'	One	1.20 - 2.50	top distal, flattish area upper 1/4 to 1/5 distal 1 mm from petiole base	1.00 - 7.00	0.25 - 1.00
" " 'Jones'	One	1.80 - 2.50	top distal, flattish area upper 1/4 to 1/5 distal touching petiole base	1.00 - 2.00	0.00 - 0.25
" " 'Monty'	One	0.80 - 2.00	top distal, flattish area upper 1/4 to 1/5 distal touching petiole base	1.00 - 5.00	0.25 - 2.00

Table 3.6 continued next page

Table 3.6. continued

Taxon	Number of shoots	ostiole width (mm)	Ostiole : position on distal side distance from petiole base	Number of bud structures visible through ostiole	Height of visible bud structures (mm)
A. *deliciosa* var. *deliciosa*					
" " 'Elmwood'	One	1.00 - 2.50	top distal, flattish area, upper 1/4 to 1/5 distal 1 mm from petiole base	3.00 - 5.00	1.00 - 3.00
A. deliciosa var. *chlorocarpa*	One	1.00 - 1.50	top distal, gentle rise upper $\frac{1}{4}$ distal 1 mm below petiole base	1.00 - 2.00	0.10 - 0.50

Footnotes :

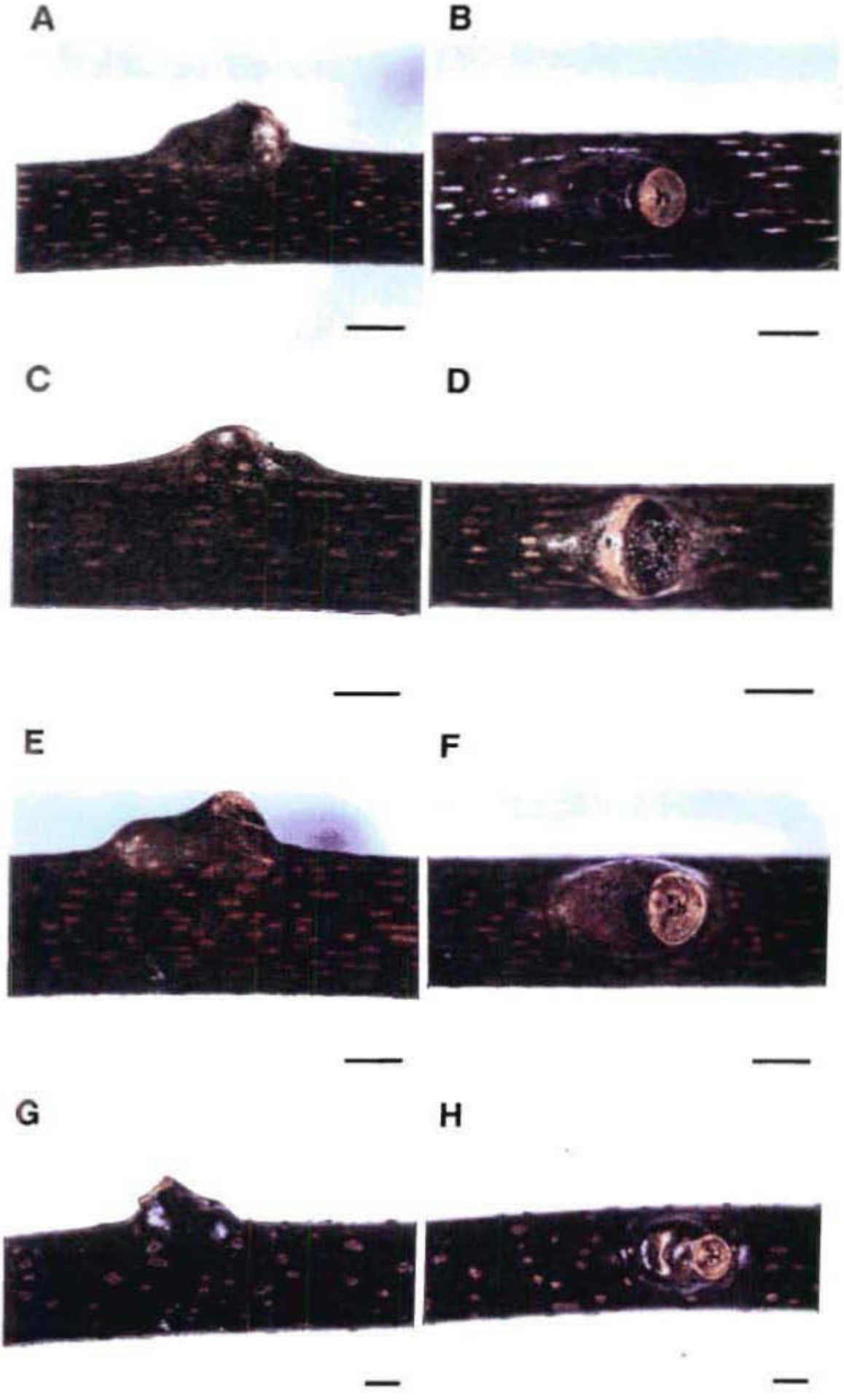
1. "mid-distal" refers to ostiole position measured from the petiole base to the base of the bud case, on the distal side.
2. "1 mm from petiole base" refers to intervening bud-case tissue between the top of the ostiole and the distal edge of the petiole base.
3. The highest value of the range is perhaps the most informative.

PLATE 3.1:

Profile and plan views of outer bud-cases of winter-dormant shoots of selected *Actinidia*, (*Leiocarpae*).

A,B *A. arguta* var. *arguta*
C,D *A. arguta* var. *purpurea*
E,F *A. arguta* var. *cordifolia*
G,H *A. kolomikta*

Bar scale = 5 mm


A
B
C
D
E
F
G
H

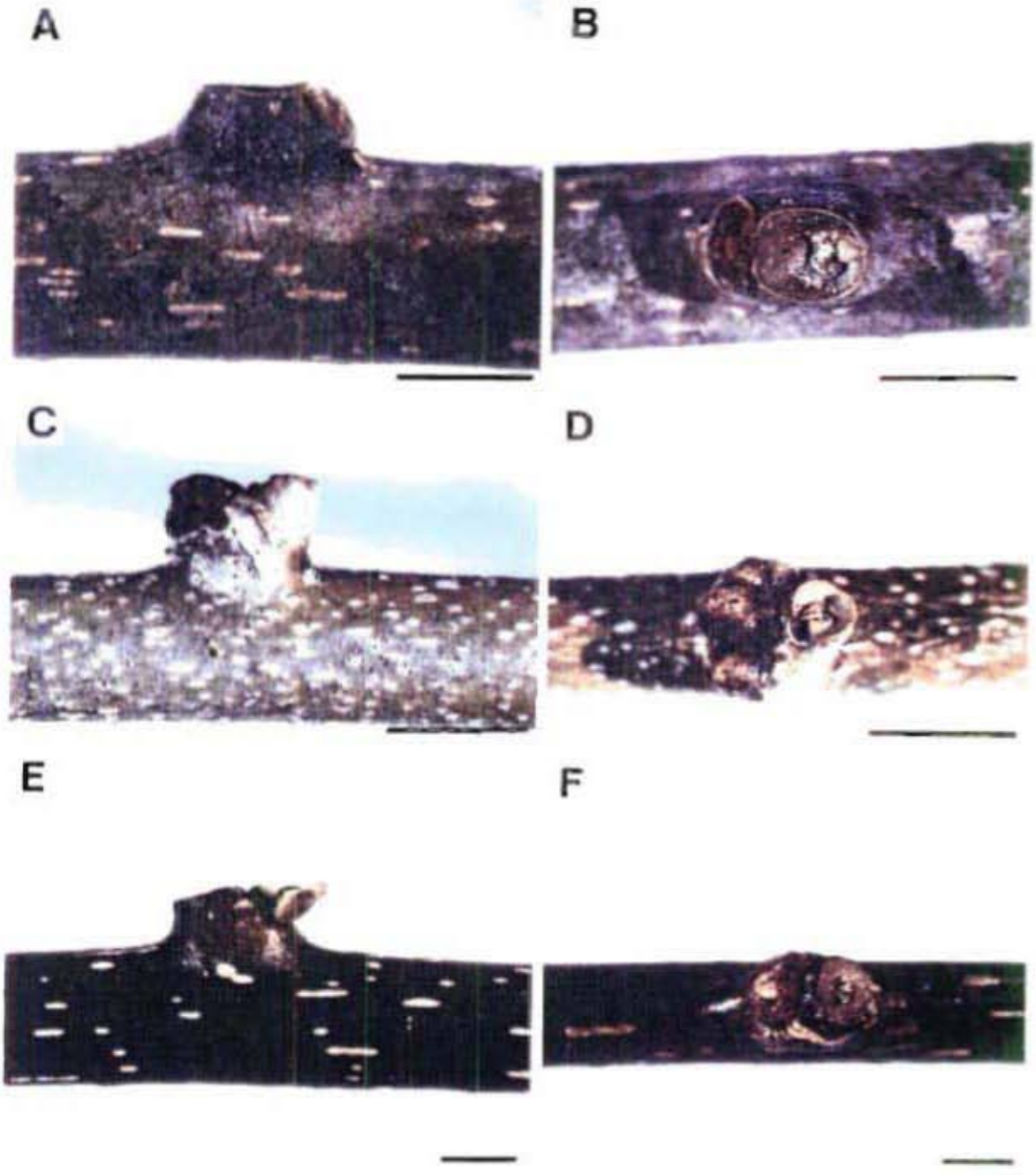


PLATE 3.2:

Profile and plan views of outer bud-cases of selected *Actinidia*.

A,B *A. rufa*, shoots tomentose.
C,D *A. callosa* var. *henryi*, 3 shoots per bud.
E,F *A. indochinensis* buds breaking early. poor dormancy

Bar scale = 5 mm

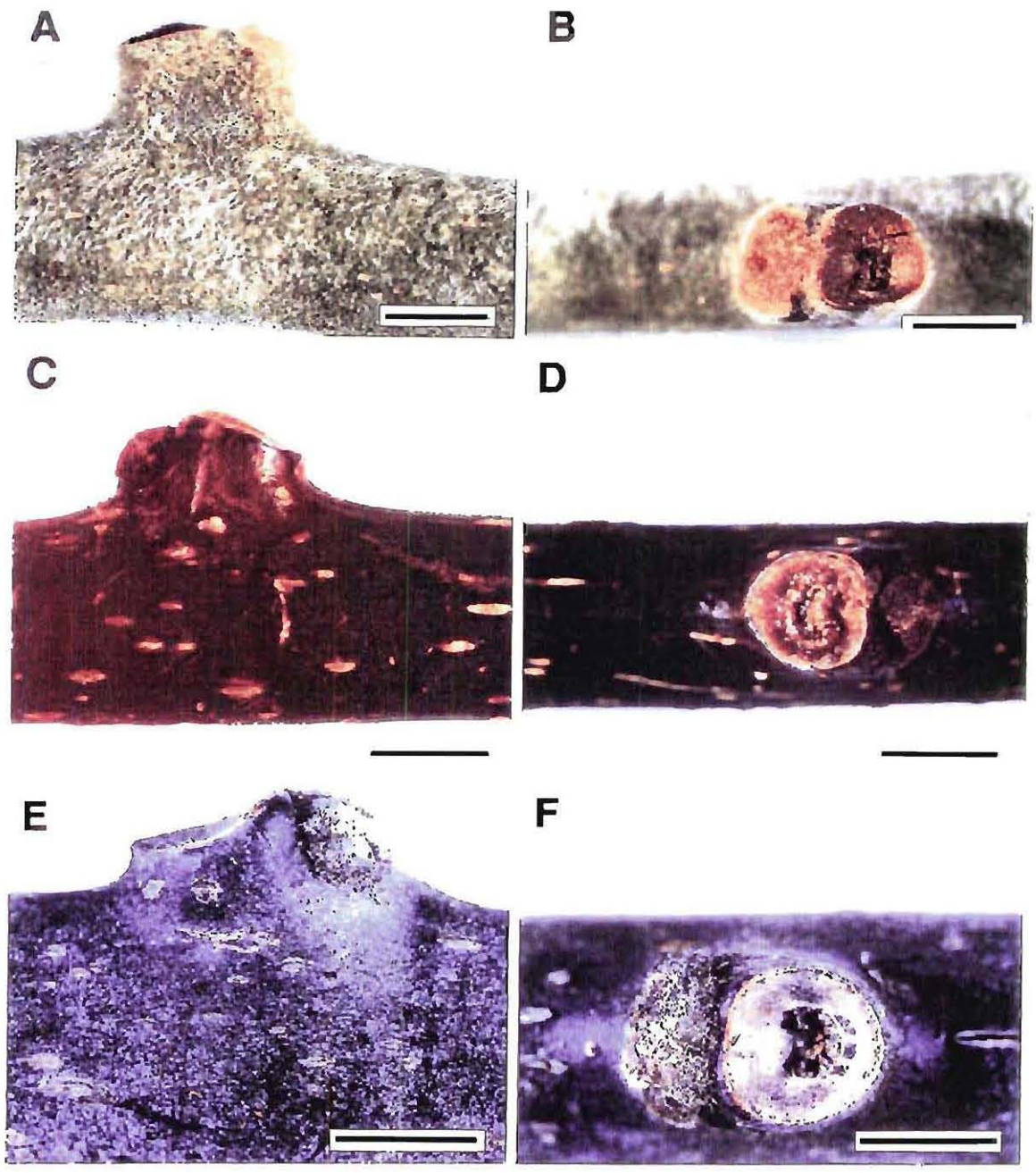


PLATE 3.3:

Profile and plan views of outer bud-cases of selected *Actinidia*, (*Stellatae* l.).

A,B *A. eriantha* shoots incanescent
C,D *A. latifolia* shoots red-brown
E,F *A. deliciosa* var. *chlorocarpa* shoots hispid tomentose; persistent hairs

Bar scale = 5 mm

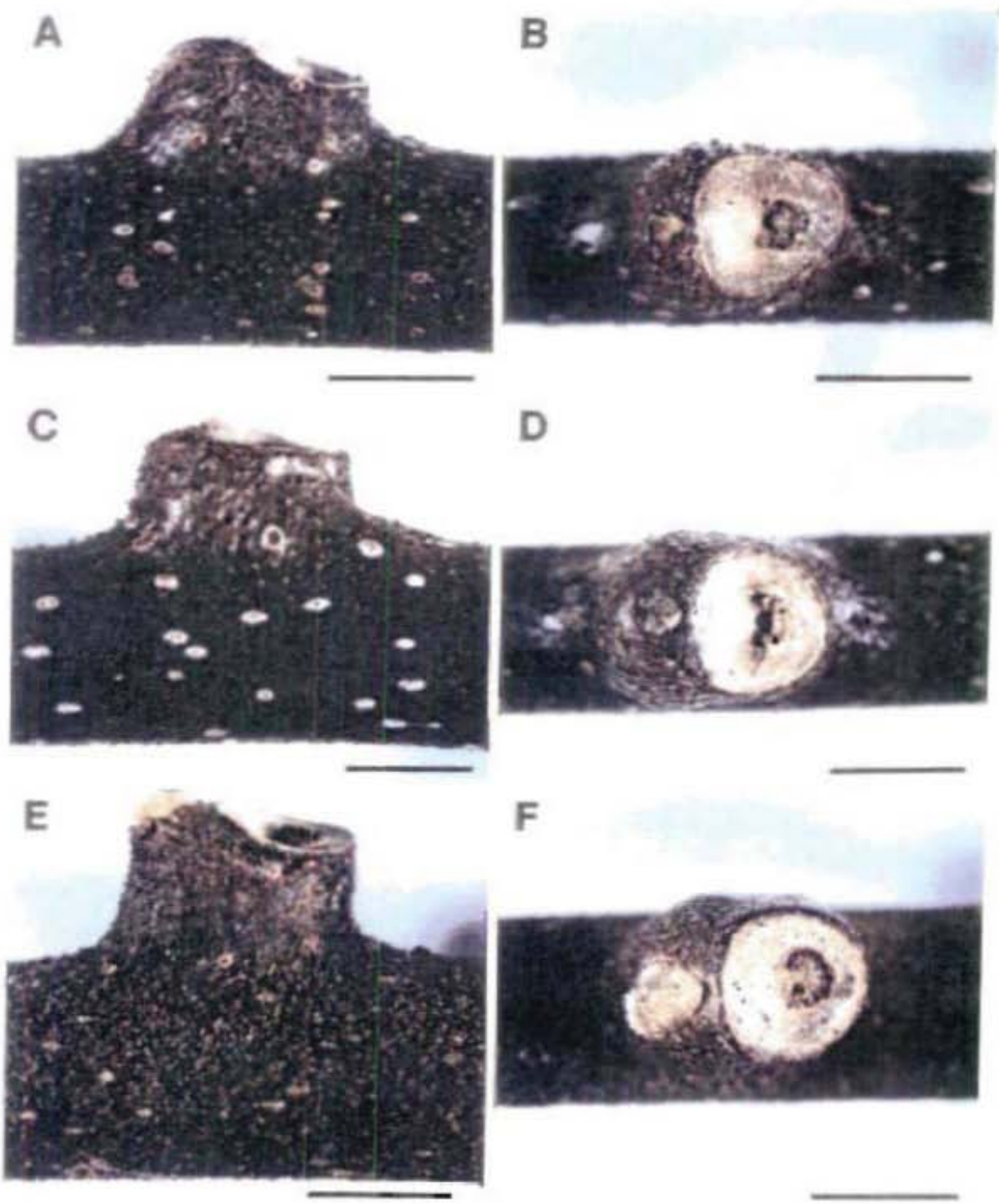


PLATE 3.4:

Profile and plan views of outer bud-cases of selected *Actinidia*, (*Stellatae* II.).

A,B *A. deliciosa* var. *deliciosa* cv. Hayward
C,D *A. deliciosa* var. *deliciosa* cv. Gracie
E,F *A. deliciosa* var. *deliciosa* cv. Elmwood

Bar scale = 5 mm

Figure 3·4·1: LENTICEL DENSITY on CANE (cm^{-2})

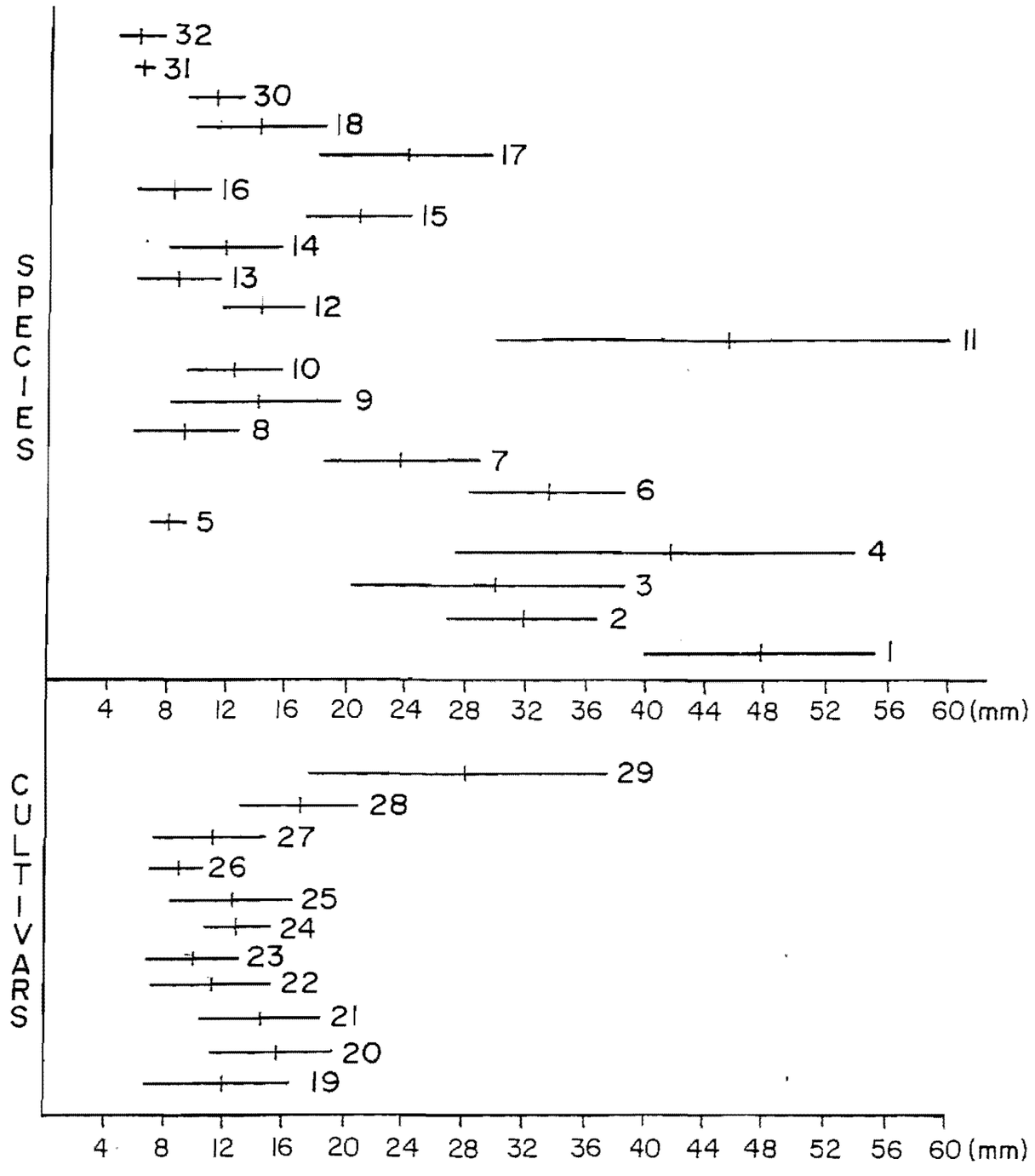
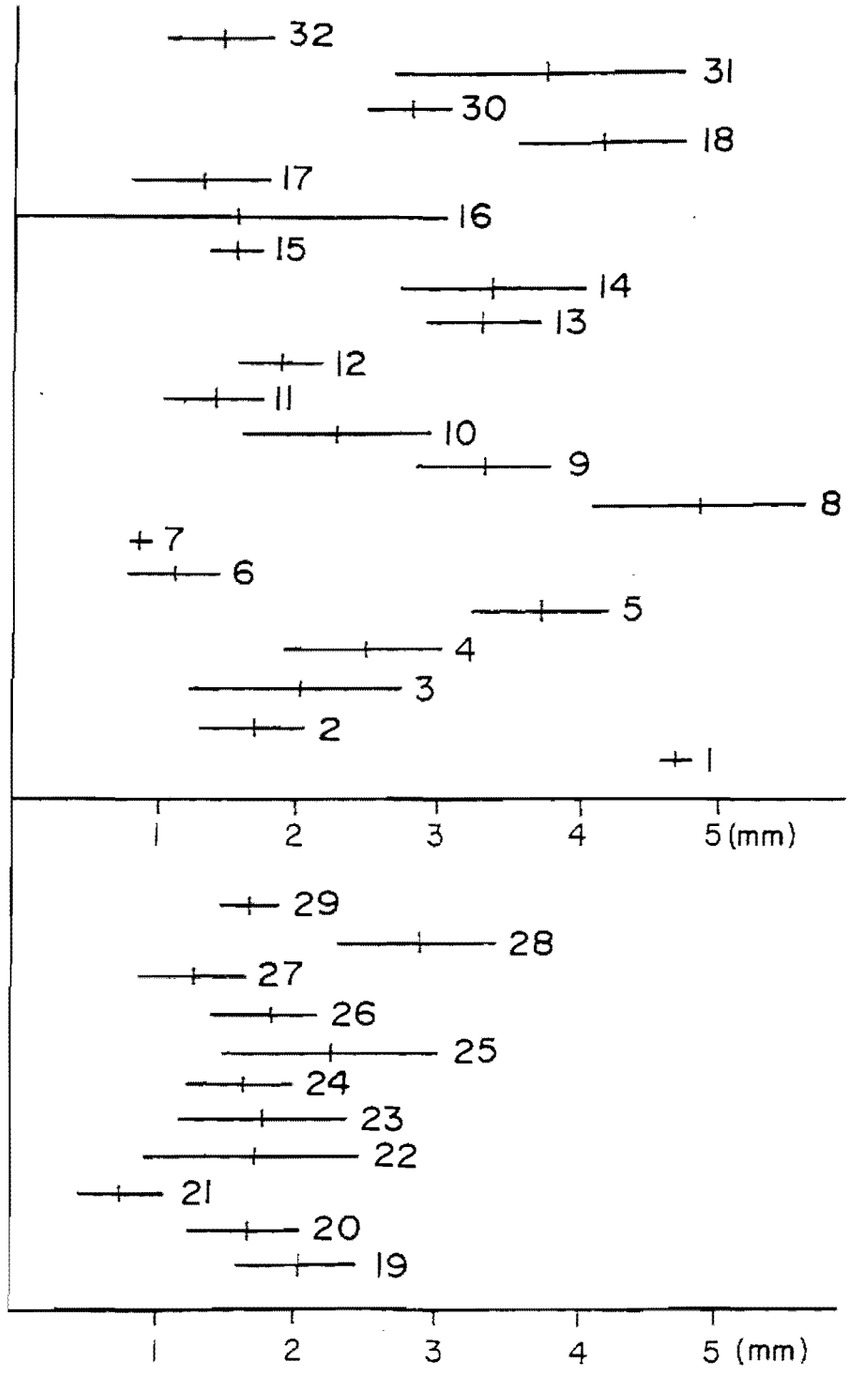


Figure 3·4·2: LONGEST LENTICEL CANE MEANS



GRAPHS OF MEANS ± 95% CONFIDENCE LIMITS, KEY TO TAXA CODES

Leiocarpae: 1 = *A. arguta var. arguta* 2 = *A. arguta* var. *cordifolia* 3 = *A. arguta* var. *giraldi* 4 = *A. arguta* var. *purpurea* 5 = *A. rufa* 6 = *A. melanandra* var. *melanandra* 7 = *A. kolomikta* 8 = *A. polygama 3/12/11* 9 = *A. polygama 3/12/9a* 10 = *A. valvata*

Maculatae: 11 = *A. callosa* var. *henyri* 12 = *A. chrysantha* 13 = *A. indochinensis 36/3/11b* 14 = *A. indochinensis 36/3/8b*

Strigosae: 15 = *A. melliana* 16 = *A. hemsleyana*

Stellatae: 17 = *A. eriantha* 18 = *A. latifolia* 19 = *A. deliciosa* 'Hayward' 20 = *A. del.* 'Bruno' 21 = *A. del.* 'Abbott' 22 = *A. del.* 'Gracie' 23 = *A. del.* 'Greensill, constricted' 24 = *A. del.* 'Allison' 25 = *A. del.* 'Matua' 26 = *A. del.* 'Jones' 27 = *A. del.* 'Monty' 28 = *A. del.* 'Elmwood' 29 = *A. del.* var. *chlorocarpa* 30 = *A. chinensis* var. *chinensis* 460/4 31 = *A. chinensis* var. *chinensis 3/6/14b* 32 = *A. chinensis* var. *chinensis* 460/9.

Figure 3·4·3: BUDLENGTH MEANS

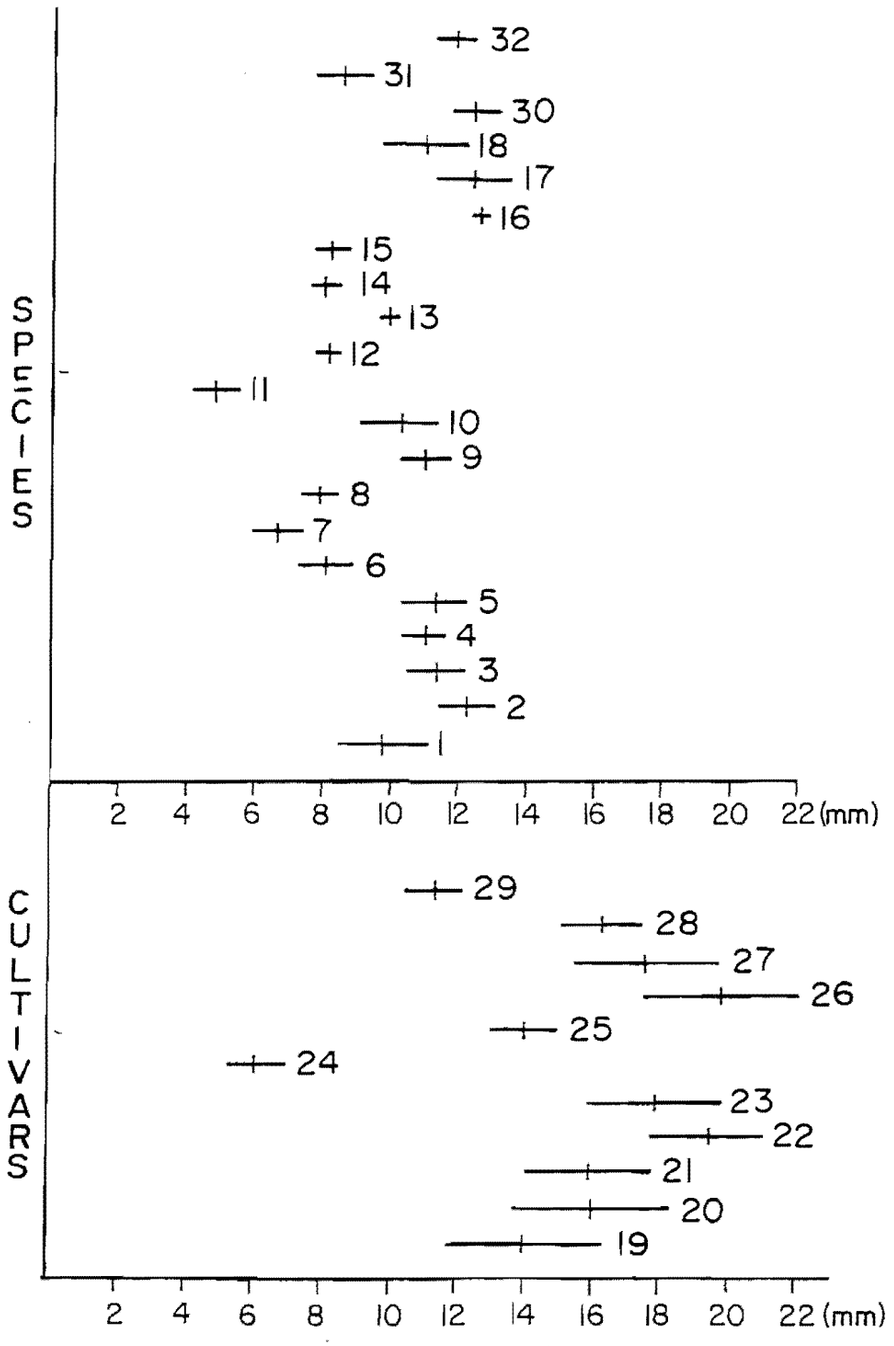


Figure 3·4·4: BUDHEIGHT MEANS

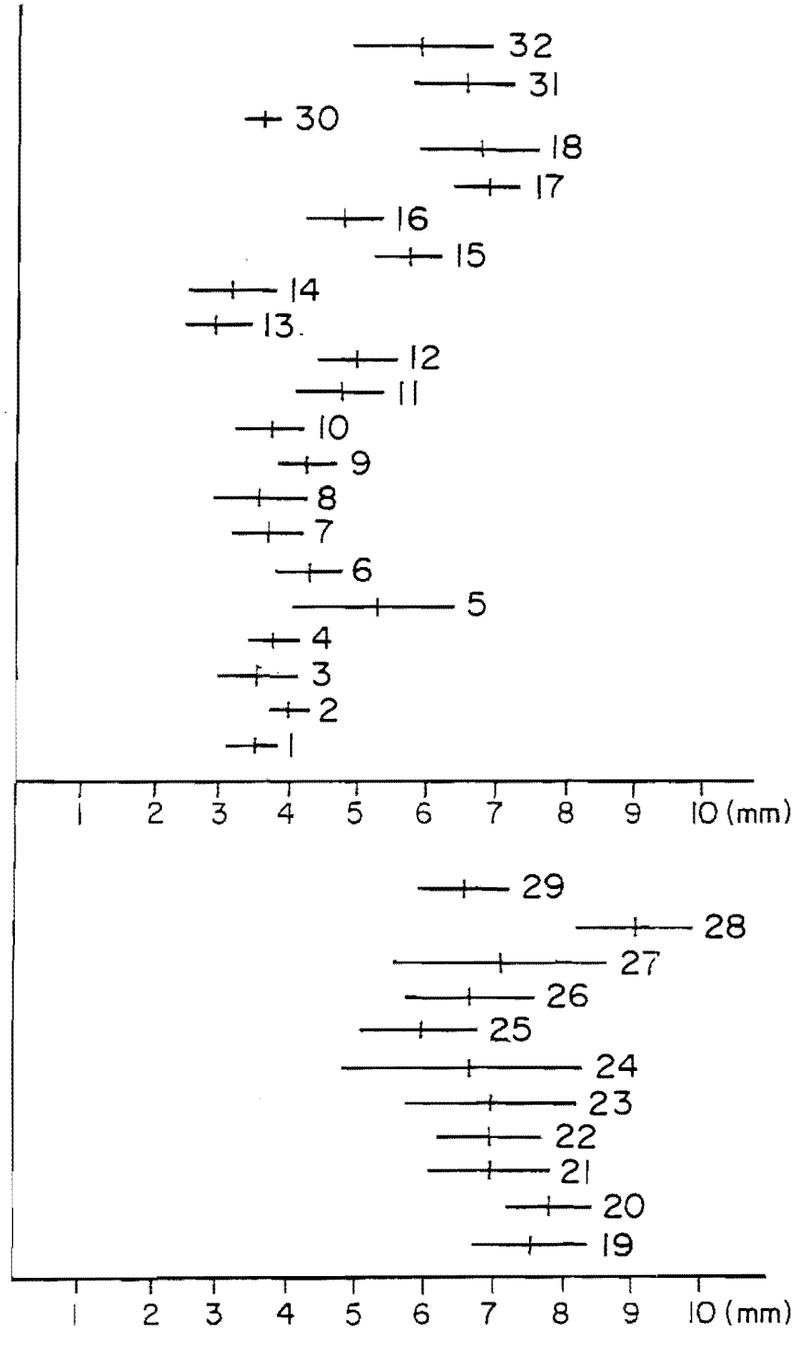
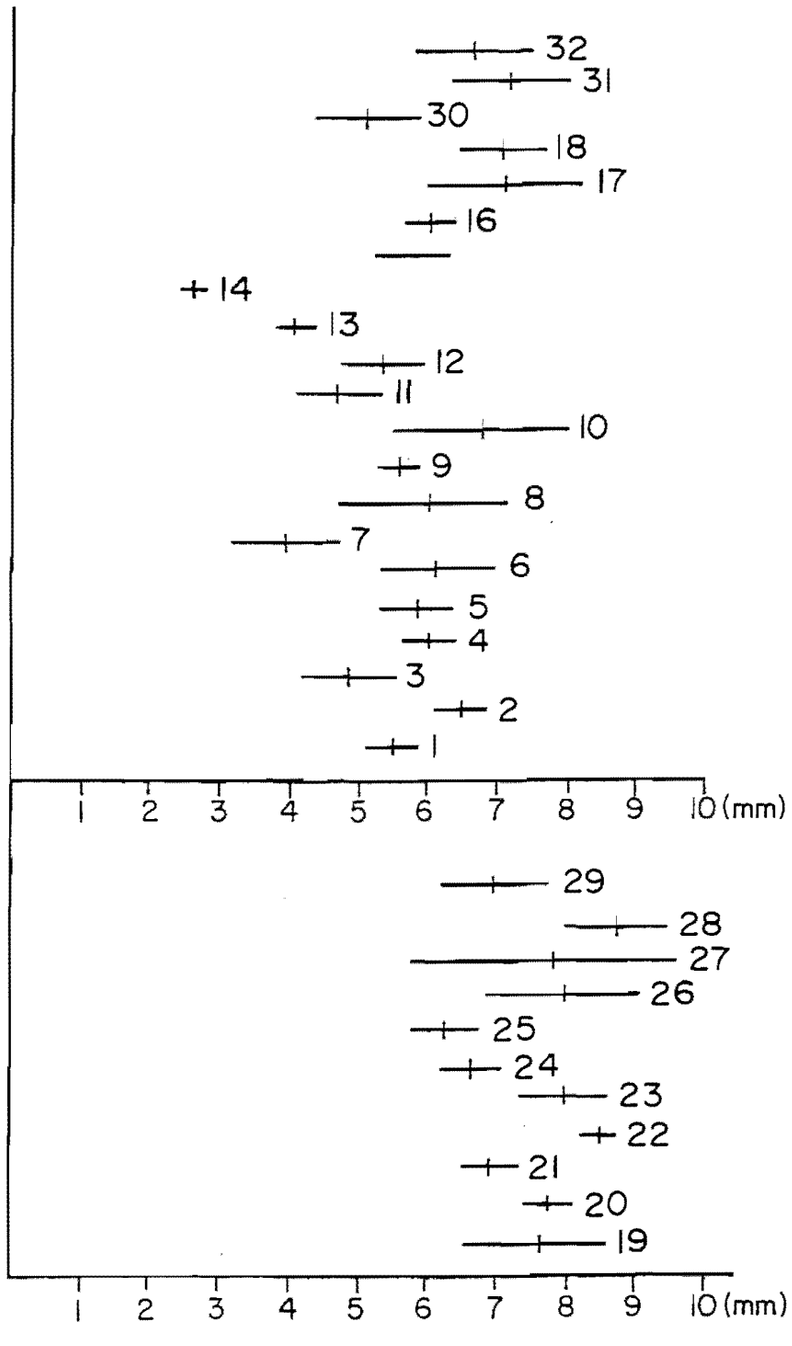


Figure 3·4·5: BUDWIDTH MEANS



GRAPHS OF MEANS ± 95% CONFIDENCE LIMITS, KEY TO TAXA CODES

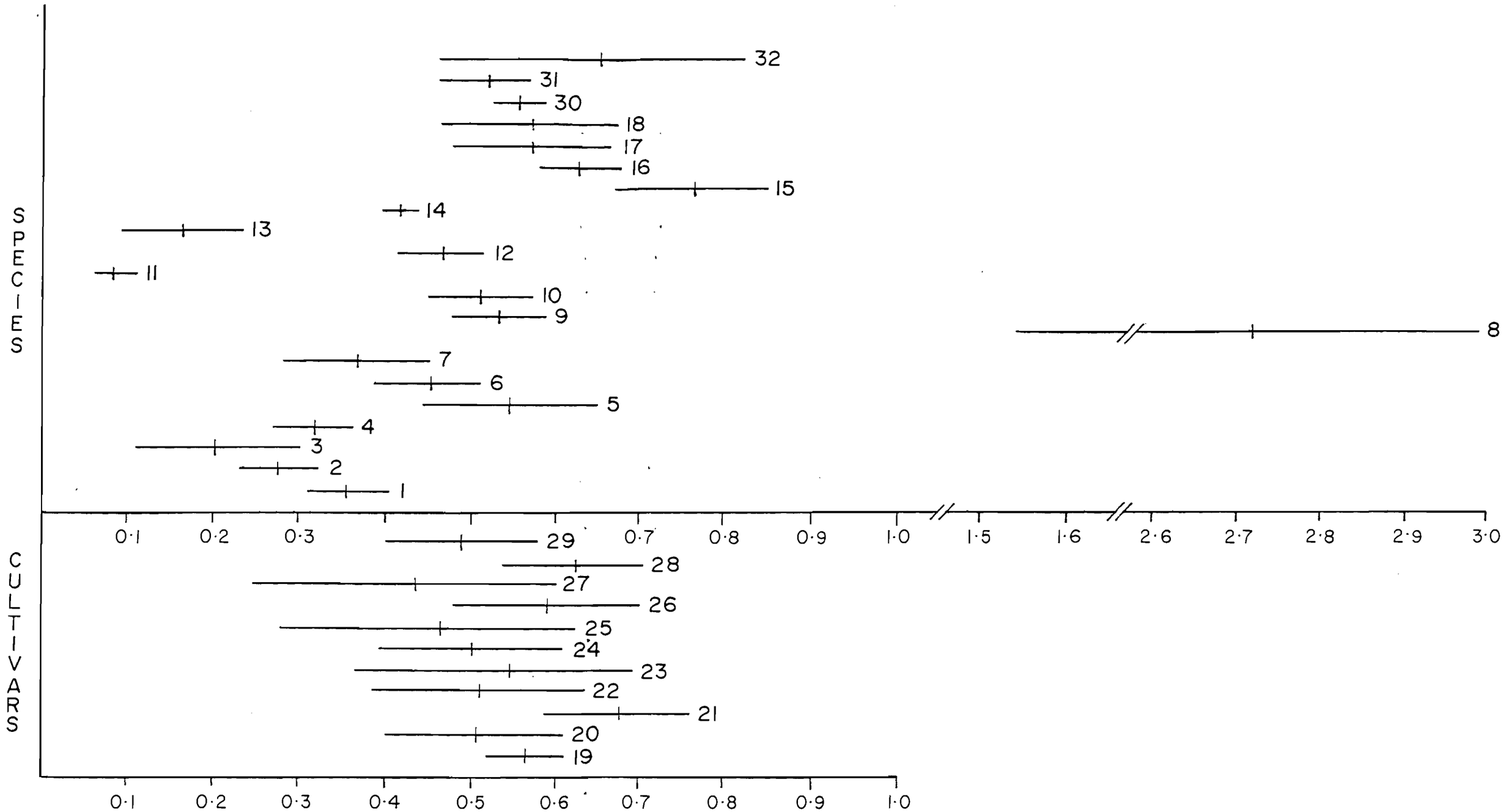
Leiocarpae: 1 = *A. arguta var. arguta* 2 = *A. arguta* var. *cordifolia* 3 = *A. arguta* var. *giraldi* 4 = *A. arguta* var. *purpurea* 5 = *A. rufa* 6 = *A. melanandra* var. *melanandra* 7 = *A. kolomikta* 8 = *A. polygama 3/12/11* 9 = *A. polygama 3/12/9a* 10 = *A. valvata*

Maculatae: 11 = *A. callosa* var. *henyri* 12 = *A. chrysantha* 13 = *A. indochinensis 36/3/11b* 14 = *A. indochinensis 36/3/8b*

Strigosae: 15 = *A. melliana* 16 = *A. hemsleyana*

Stellatae: 17 = *A. eriantha* 18 = *A. latifolia* 19 = *A. deliciosa* 'Hayward' 20 = *A. del.* 'Bruno' 21 = *A. del.* 'Abbott' 22 = *A. del.* 'Gracie' 23 = *A. del.* 'Greensill, constricted' 24 = *A. del.* 'Allison' 25 = *A. del.* 'Matua' 26 = *A. del.* 'Jones' 27 = *A. del.* 'Monty' 28 = *A. del.* 'Elmwood' 29 = *A. del.* var. *chlorocarpa* 30 = *A. chinensis* var. *chinensis* 460/4 31 = *A. chinensis* var. *chinensis 3/6/14b* 32 = *A. chinensis* var. *chinensis* 460/9.

Figure 3·4·6: BUDLENGTH to BUDHEIGHT (BUDCASE SHAPE RATIO) RATIO MEANS



GRAPHS OF MEANS ± 95% CONFIDENCE LIMITS, KEY TO TAXA CODES

Leiocarpae: 1 = *A. arguta var. arguta* 2 = *A. arguta* var. *cordifolia* 3 = *A. arguta* var. *giraldi* 4 = *A. arguta* var. *purpurea* 5 = *A. rufa* 6 = *A. melanandra* var. *melanandra* 7 = *A. kolomikta* 8 = *A. polygama 3/12/11* 9 = *A. polygama 3/12/9a* 10 = *A. valvata*

Maculatae: 11 = *A. callosa* var. *henyri* 12 = *A. chrysantha* 13 = *A. indochinensis 36/3/11b* 14 = *A. indochinensis 36/3/8b*

Strigosae: 15 = *A. melliana* 16 = *A. hemsleyana*

Stellatae: 17 = *A. eriantha* 18 = *A. latifolia* 19 = *A. deliciosa* 'Hayward' 20 = *A. del.* 'Bruno' 21 = *A. del.* 'Abbott' 22 = *A. del.* 'Gracie' 23 = *A. del.* 'Greensill, constricted' 24 = *A. del.* 'Allison' 25 = *A. del.* 'Matua' 26 = *A. del.* 'Jones' 27 = *A. del.* 'Monty' 28 = *A. del.* 'Elmwood' 29 = *A. del.* var. *chlorocarpa* 30 = *A. chinensis* var. *chinensis* 460/4 31 = *A. chinensis* var. *chinensis 3/6/14b* 32 = *A. chinensis* var. *chinensis* 460/9.

Figure 3·4·7: B.T.O.H. DISTANCE MEANS

B.T.O.H. = Base to highest point
= horizontal distance from base of bud to bud summit

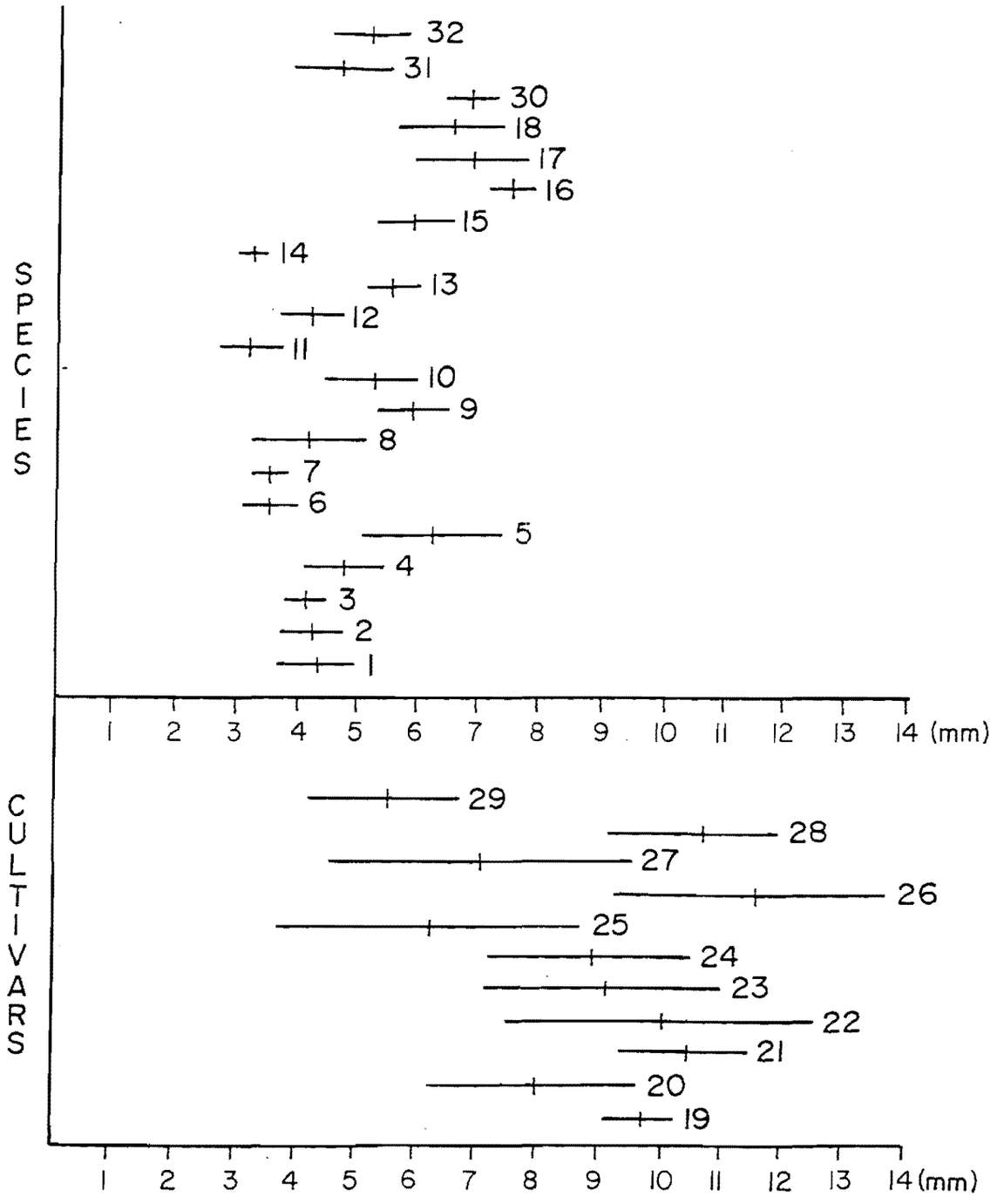
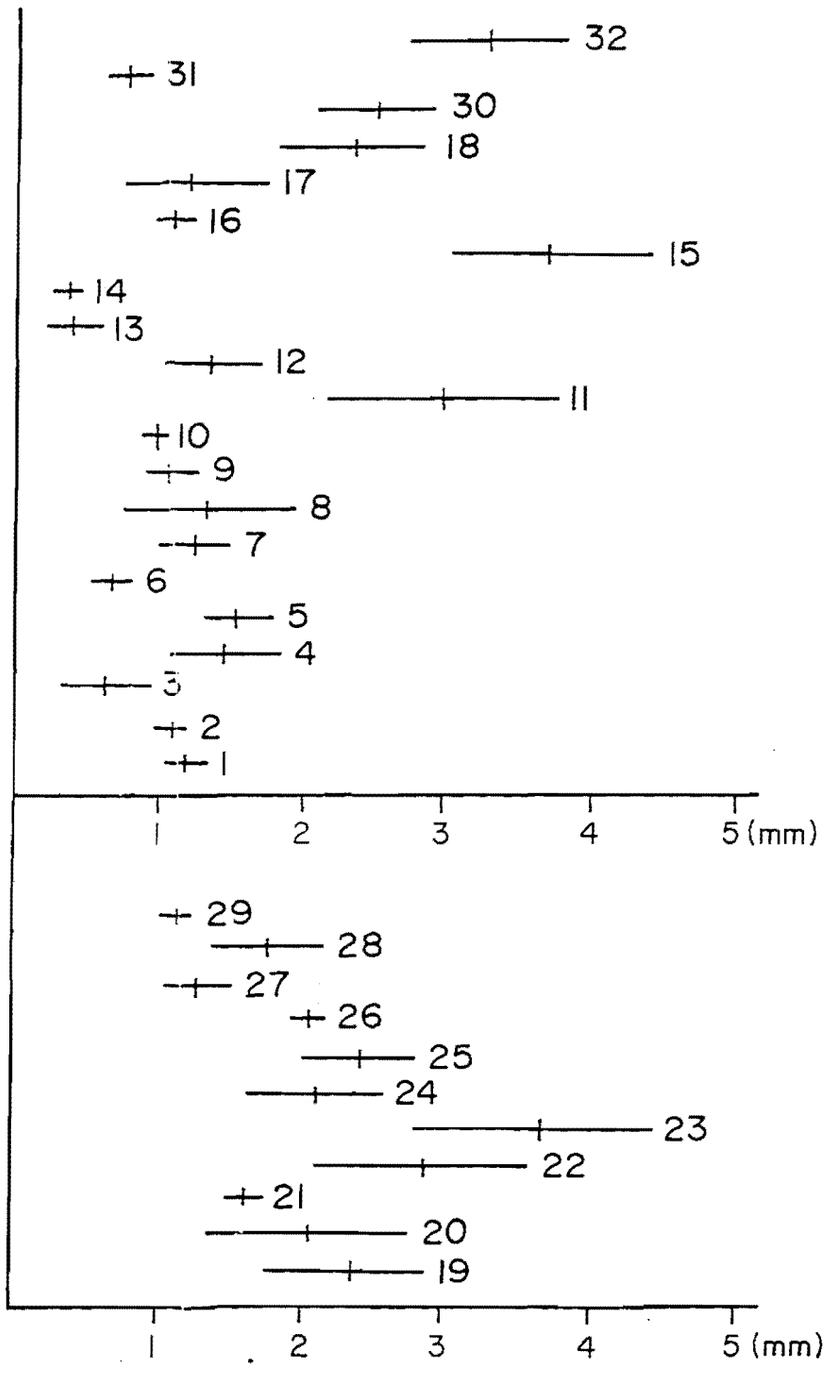


Figure 3·4·8: DEPTH of PETIOLE SCAR MEANS



GRAPHS OF MEANS ±95% CONFIDENCE LIMITS, KEY TO TAXA CODES

Leiocarpae: 1 = *A. arguta var. arguta* 2 = *A. arguta* var. *cordifolia* 3 = *A. arguta* var. *giraldi* 4 = *A. arguta* var. *purpurea* 5 = *A. rufa* 6 = *A. melanandra* var. *melanandra* 7 = *A. kolomikta* 8 = *A. polygama 3/12/11* 9 = *A. polygama 3/12/9a* 10 = *A. valvata*

Maculatae: 11 = *A. callosa* var. *henyri* 12 = *A. chrysantha* 13 = *A. indochinensis 36/3/11b* 14 = *A. indochinensis 36/3/8b*

Strigosae: 15 = *A. melliana* 16 = *A. hemsleyana*

Stellatae: 17 = *A. eriantha* 18 = *A. latifolia* 19 = *A. deliciosa* 'Hayward' 20 = *A. del.* 'Bruno' 21 = *A. del.* 'Abbott' 22 = *A. del.* 'Gracie' 23 = *A. del.* 'Greensill, constricted' 24 = *A. del.* 'Allison' 25 = *A. del.* 'Matua' 26 = *A. del.* 'Jones' 27 = *A. del.* 'Monty' 28 = *A. del.* 'Elmwood' 29 = *A. del.* var. *chlorocarpa* 30 = *A. chinensis* var. *chinensis* 460/4 31 = *A. chinensis* var. *chinensis 3/6/14b* 32 = *A. chinensis* var. *chinensis* 460/9.

Figure 3·4·9: OSTIOLE WIDTH MEANS

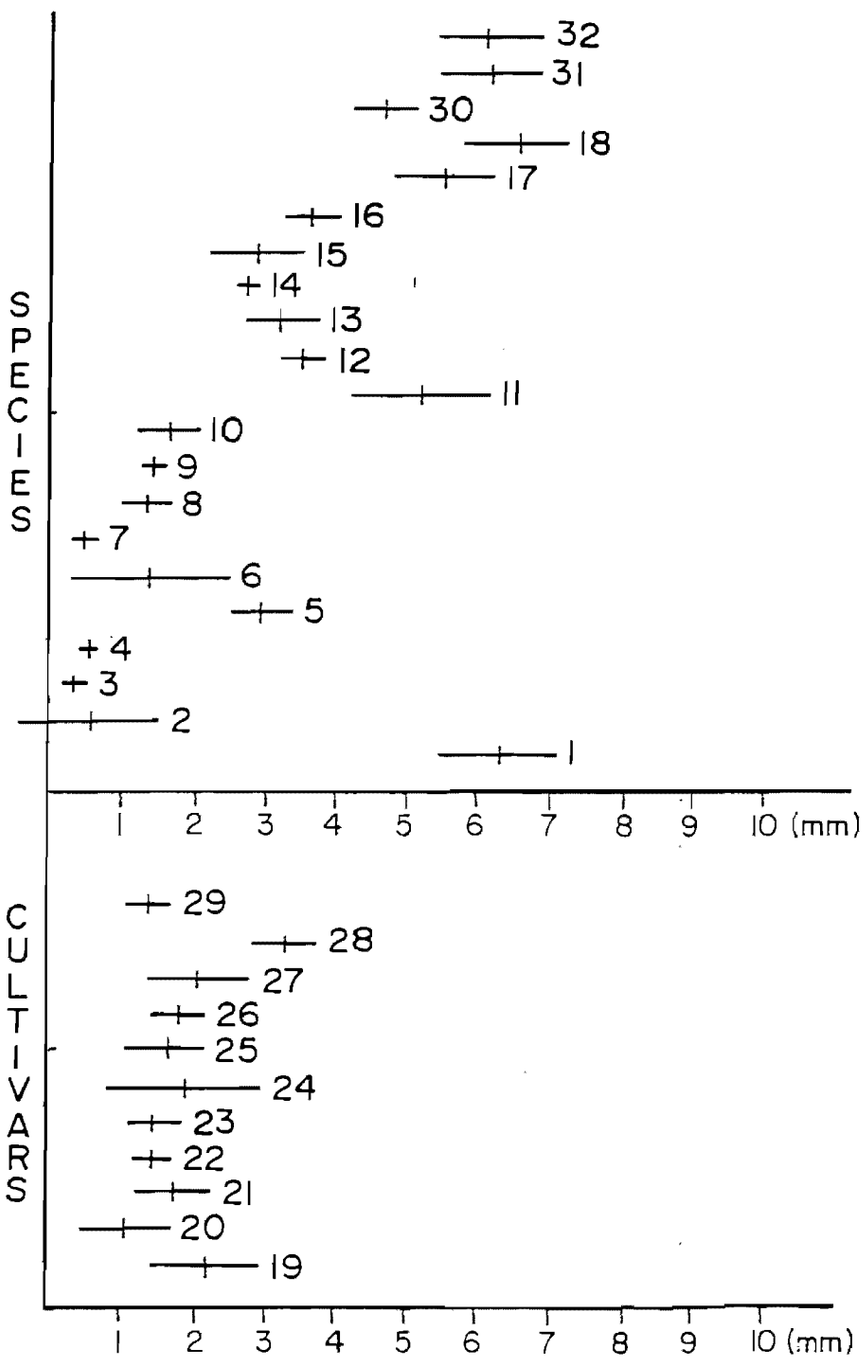
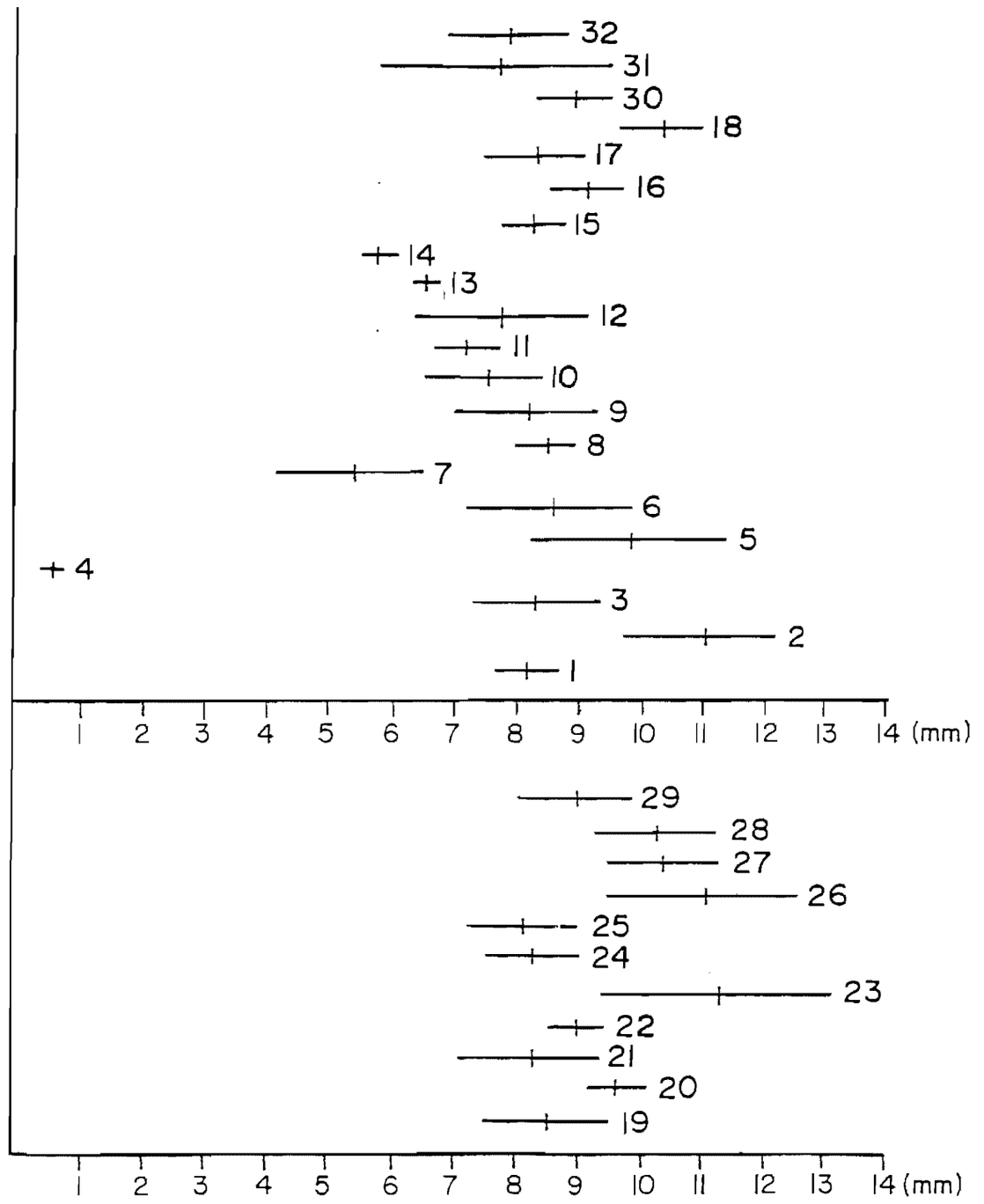


Figure 3·4·10: CANE DIAMETER MEANS



GRAPHS OF MEANS ± 95% CONFIDENCE LIMITS, KEY TO TAXA CODES

Leiocarpae: 1 = *A. arguta var. arguta* 2 = *A. arguta* var. *cordifolia* 3 = *A. arguta* var. *giraldi* 4 = *A. arguta* var. *purpurea* 5 = *A. rufa* 6 = *A. melanandra* var. *melanandra* 7 = *A. kolomikta* 8 = *A. polygama 3/12/11* 9 = *A. polygama 3/12/9a* 10 = *A. valvata*

Maculatae: 11 = *A. callosa* var. *henyri* 12 = *A. chrysantha* 13 = *A. indochinensis 36/3/11b* 14 = *A. indochinensis 36/3/8b*

Strigosae: 15 = *A. melliana* 16 = *A. hemsleyana*

Stellatae: 17 = *A. eriantha* 18 = *A. latifolia* 19 = *A. deliciosa* 'Hayward' 20 = *A. del.* 'Bruno' 21 = *A. del.* 'Abbott' 22 = *A. del.* 'Gracie' 23 = *A. del.* 'Greensill, constricted' 24 = *A. del.* 'Allison' 25 = *A. del.* 'Matua' 26 = *A. del.* 'Jones' 27 = *A. del.* 'Monty' 28 = *A. del.* 'Elmwood' 29 = *A. del.* var. *chlorocarpa* 30 = *A. chinensis* var. *chinensis* 460/4 31 = *A. chinensis* var. *chinensis 3/6/14b* 32 = *A. chinensis* var. *chinensis* 460/9.

Figure 3·4·11: HEIGHT of VISIBLE BUD STRUCTURES MEANS

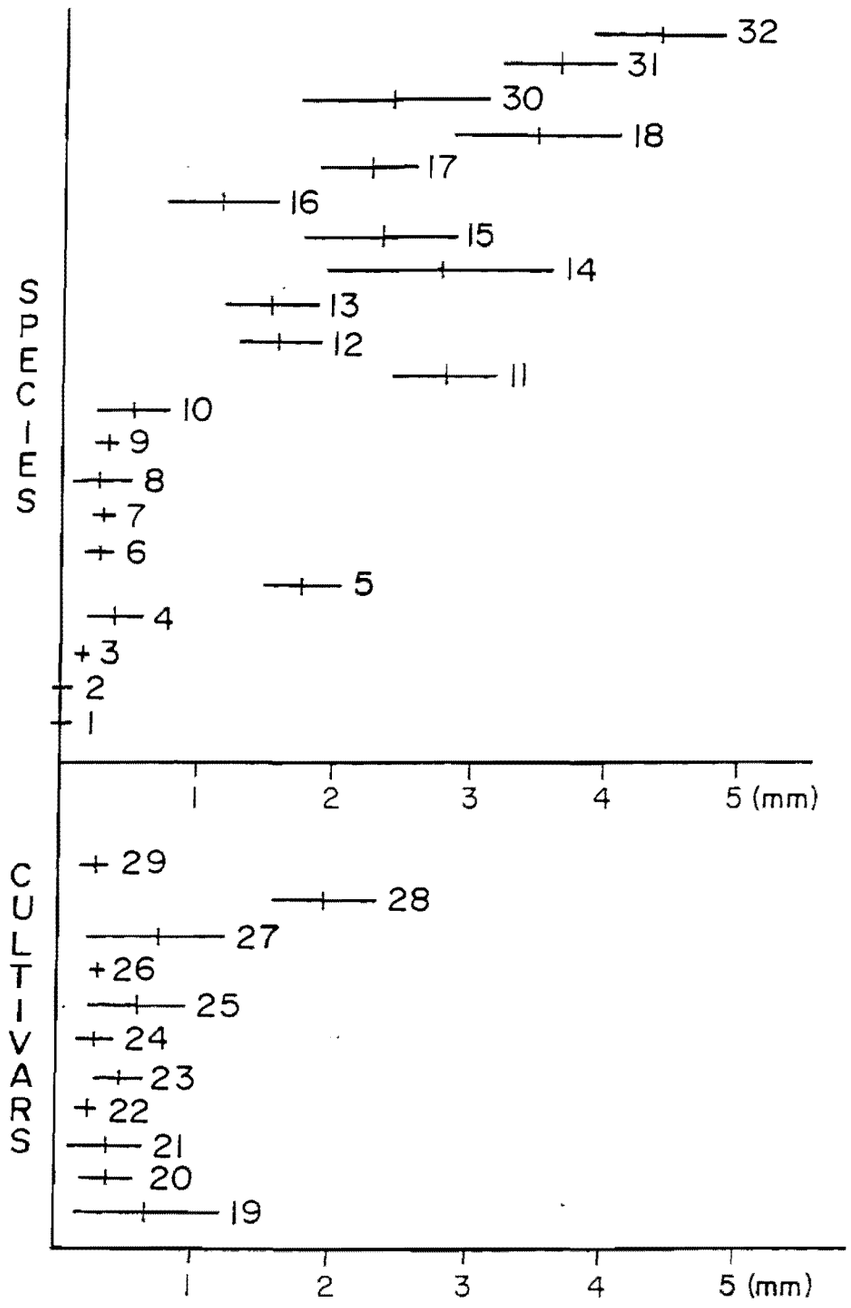


Figure 3·4·12: NUMBER of VISIBLE BUD STRUCTURES (OSTIOLE)

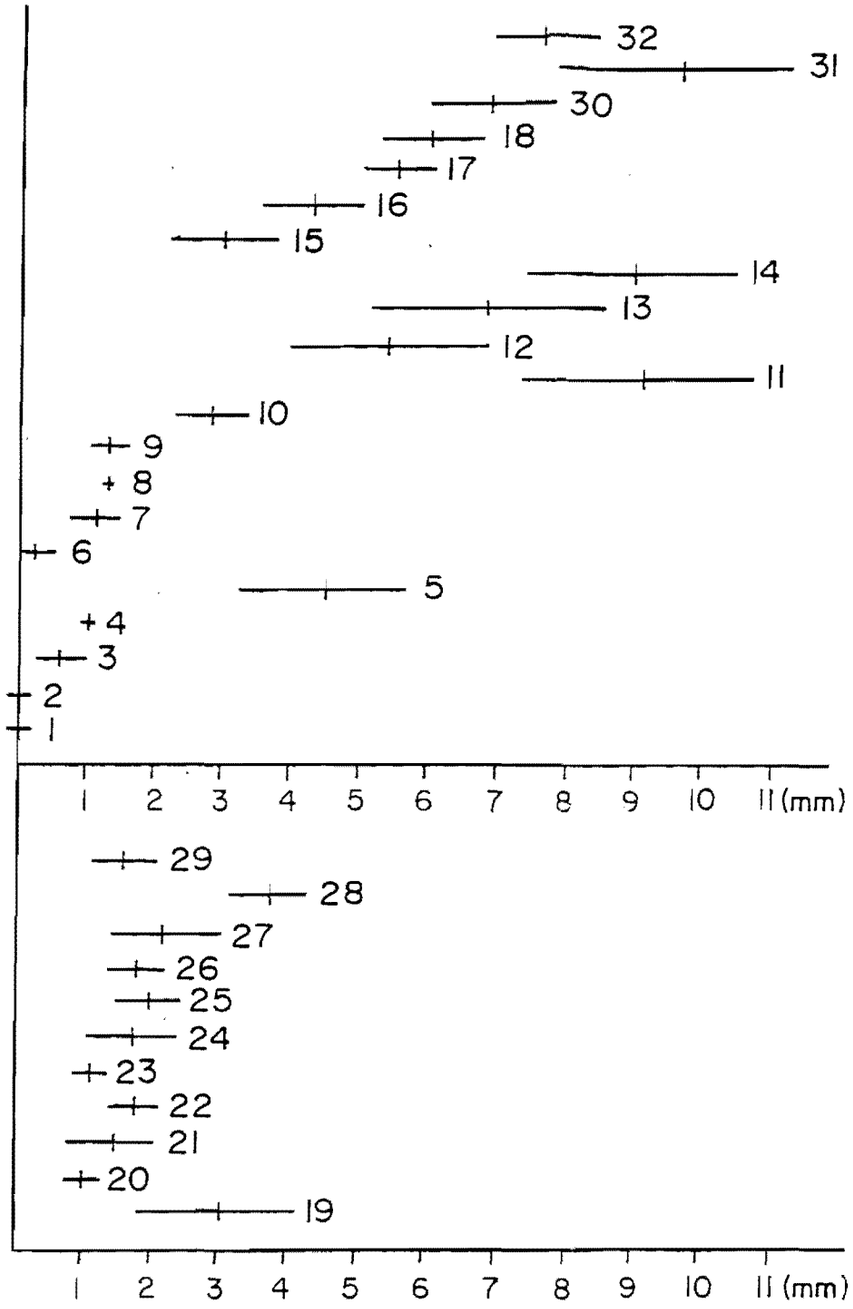
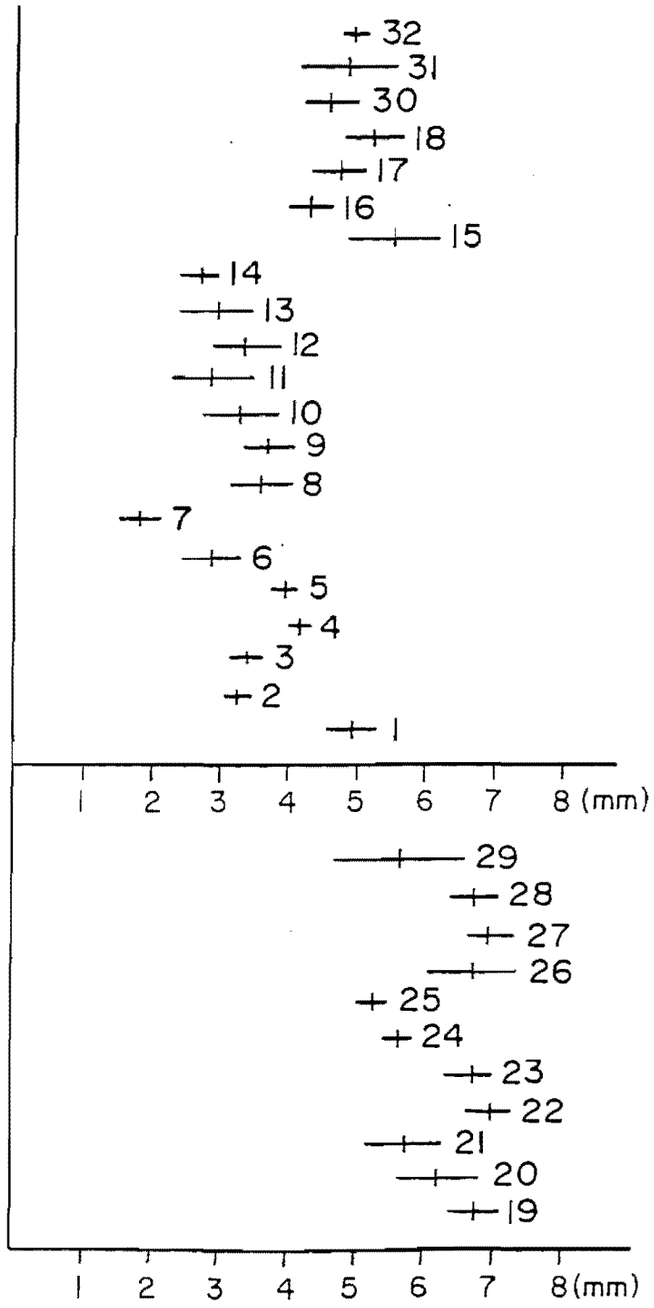


Figure 3·4·13: L.P.D. PETIOLE BASE MEANS



GRAPHS OF MEANS ± 95% CONFIDENCE LIMITS, KEY TO TAXA CODES

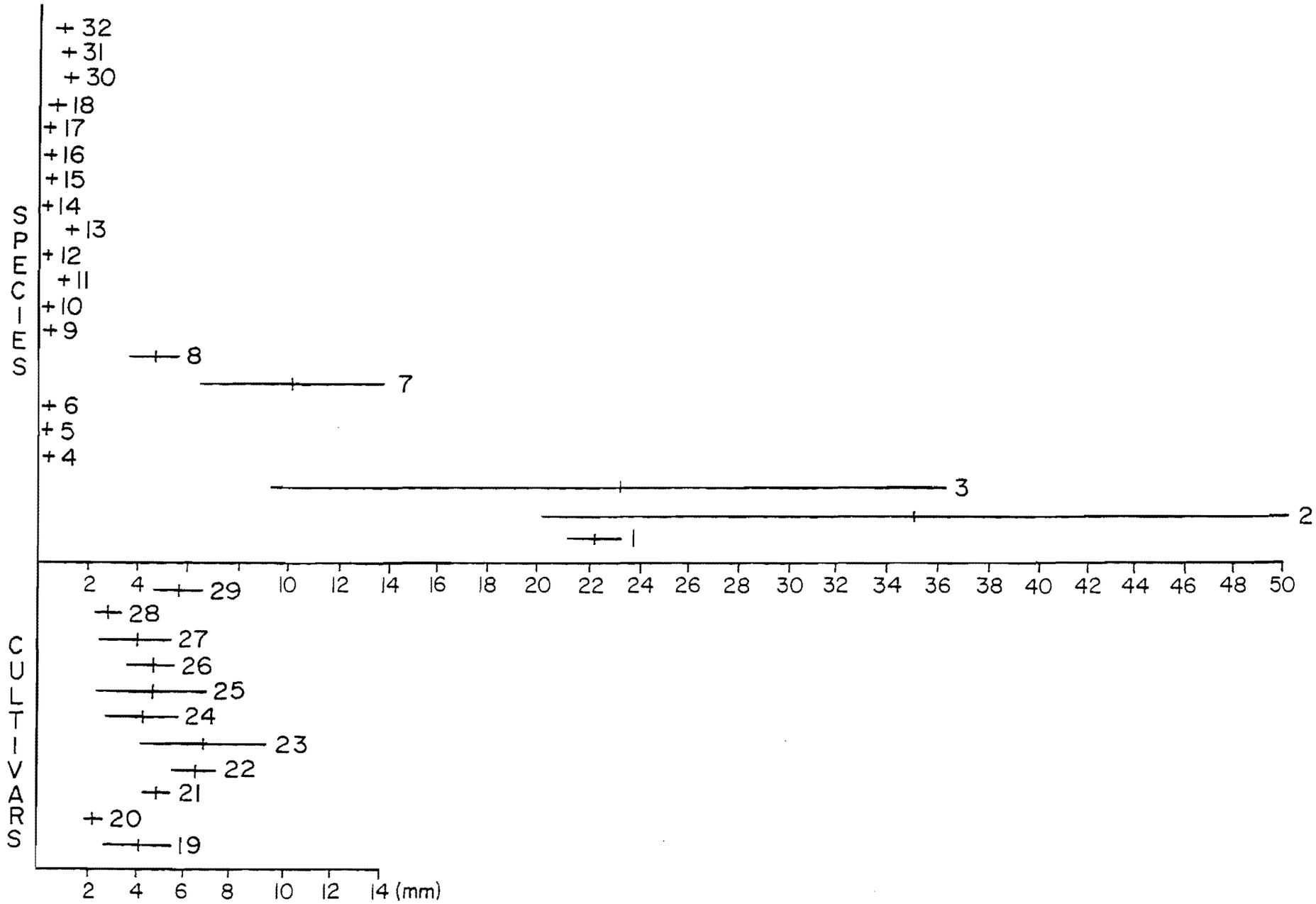
Leiocarpae: 1 = *A. arguta var. arguta* 2 = *A. arguta* var. *cordifolia* 3 = *A. arguta* var. *giraldi* 4 = *A. arguta* var. *purpurea* 5 = *A. rufa* 6 = *A. melanandra* var. *melanandra* 7 = *A. kolomikta* 8 = *A. polygama 3/12/11* 9 = *A. polygama 3/12/9a* 10 = *A. valvata*

Maculatae: 11 = *A. callosa* var. *henyri* 12 = *A. chrysantha* 13 = *A. indochinensis 36/3/11b* 14 = *A. indochinensis 36/3/8b*

Strigosae: 15 = *A. melliana* 16 = *A. hemsleyana*

Stellatae: 17 = *A. eriantha* 18 = *A. latifolia* 19 = *A. deliciosa* 'Hayward' 20 = *A. del.* 'Bruno' 21 = *A. del.* 'Abbott' 22 = *A. del.* 'Gracie' 23 = *A. del.* 'Greensill, constricted' 24 = *A. del.* 'Allison' 25 = *A. del.* 'Matua' 26 = *A. del.* 'Jones' 27 = *A. del.* 'Monty' 28 = *A. del.* 'Elmwood' 29 = *A. del.* var. *chlorocarpa* 30 = *A. chinensis* var. *chinensis* 460/4 31 = *A. chinensis* var. *chinensis 3/6/14b* 32 = *A. chinensis* var. *chinensis* 460/9.

Figure 3·4·14: RATIO of BUDCASE WIDTH to OSTIOLE WIDTH MEANS



GRAPHS OF MEANS ± 95% CONFIDENCE LIMITS, KEY TO TAXA CODES

Leiocarpae: 1 = *A. arguta var. arguta* 2 = *A. arguta* var. *cordifolia* 3 = *A. arguta* var. *giraldi* 4 = *A. arguta* var. *purpurea* 5 = *A. rufa* 6 = *A. melanandra* var. *melanandra* 7 = *A. kolomikta* 8 = *A. polygama 3/12/11* 9 = *A. polygama 3/12/9a* 10 = *A. valvata*

Maculatae: 11 = *A. callosa* var. *henyri* 12 = *A. chrysantha* 13 = *A. indochinensis 36/3/11b* 14 = *A. indochinensis 36/3/8b*

Strigosae: 15 = *A. melliana* 16 = *A. hemsleyana*

Stellatae: 17 = *A. eriantha* 18 = *A. latifolia* 19 = *A. deliciosa* 'Hayward' 20 = *A. del.* 'Bruno' 21 = *A. del.* 'Abbott' 22 = *A. del.* 'Gracie' 23 = *A. del.* 'Greensill, constricted' 24 = *A. del.* 'Allison' 25 = *A. del.* 'Matua' 26 = *A. del.* 'Jones' 27 = *A. del.* 'Monty' 28 = *A. del.* 'Elmwood' 29 = *A. del.* var. *chlorocarpa* 30 = *A. chinensis* var. *chinensis* 460/4 31 = *A. chinensis* var. *chinensis 3/6/14b* 32 = *A. chinensis* var. *chinensis* 460/9.

3.3.2 Cluster analysis of winter shoot characters

The 21 characters derived from winter shoots and employed in cluster analysis are detailed in Section 3.3.1 of the text. The characters selected and coded for cluster analysis are listed in Appendix 3.1.

3.3.2.1 *Clustering by average-linkage method*

Clustering by the method of average-linkage produces cohesive groupings with a minimal number of outliers (Figure 3.5).

The O.T.Us separate into four distinctive clusters "A" to "D" at a similarity level of 0.72 with *A. callosa* var. *henryi* as the sole "outlier".

Cluster "A" forms at a similarity level of *ca.* 0.73 and includes three well-differentiated subclusters. Subcluster "1" forms at a similarity of 0.87 and includes both genotypes of *A. polygama* together with *A. valvata*. The second subcluster "2" comprises a varied assemblage of *A. rufa*, *A. hemsleyana*, A. *chrysantha* and *A. melliana*, which unite at a high similarity level of 0.80. Subcluster "3" includes three morphologically similar varieties of *A. arguta:* vars. *arguta, giraldii* and *purpurea* in group "a", which are separated more distantly from *A. arguta* var. *cordifolia*, *A. melanandra* and *A. kolomikta*. Subcluster "3" is defined at a similarity level of 0.80.

Cluster "B" includes both genotypes of *A. indochinensis*, which aggregate at a similarity level of 0.85.

Cluster "C" forms at a similarity level of 0.81 and this includes three clearly defined subclusters "4" to "6". Subcluster "4" arises at a similarity of 0.86 and includes four pistillate cvs of *A. deliciosa* var. *deliciosa*, namely, 'Greensill', 'Gracie', 'Jones' and 'Monty'. Subcluster "5" includes *A. deliciosa* var. *deliciosa:* 'Bruno', Abbott' and 'Allison', together with the pistillate cultivar 'Matua' and variety *chlorocarpa.* Subcluster "6" includes *A. deliciosa* vars. *deliciosa* 'Hayward' and 'Elmwood'.

Cluster "D" forms at a similarity level of 0.74 and this includes *A. latifolia* and three genotypes of *A. chinensis* var. *chinensis* as group "7", together with the *A. eriantha* at a much lower level of similarity.

3.3.2.2 *Clustering by single-linkage method*

Cluster analysis by the method of single-linkage generates mainly cohesive groups with evidence of "chaining" at lower levels of similarity. More "outliers" are produced than in average-linkage clustering.

The composition of the major clusters "A" to "D" is basically similar in both dendrograms, except that single-linkage (Figure 3.6) shifts the groupings of

O.T.U's, which enter clusters at low levels of similarity, relative to other O.T.Us. *A. melliana* formerly of subcluster "2", now joins cluster "A" at a similarity level of 0.70. *A. eriantha* which previously belonged to subcluster "7", now joins *A. callosa* var. *henryi* as a highly distinctive "outlier".

3.3.2.3 *Cluster analysis of a reduced number of taxa using average-linkage*

Cluster analysis can be markedly affected by the information content of the O.T.Us being clustered. The robustness of the major groups can be tested by deliberate removal of O.T.Us (Figures 3.7, 3.8). Cluster analysis of the reduced data set was conducted with the same set of winter shoot characters which were used previously in Figures 3.5 and 3.6.

Four major clusters "A" to "D" arise at a similarity level of 0.51. The membership of subclusters "1" to "7" mostly agrees with those clusters derived from the full set of O.T.Us (Figures 3.5, 3.6).

Cluster "A" has three components : subcluster "1" including *A. polygama* and *A. valvata* of the *Leiocarpae* and the other *Leiocarpae* (series *Lamellatae*) occur in subcluster "3". Subcluster "2" is a mixed assemblage of *Maculatae* and *Strigosae*.

Cluster "B" which formerly included both genotypes of *A. indochinensis*, now includes *A. callosa* var. *henryi* and *A. indochinensis* 36/3/8b.

Cluster "C" contains the infraspecific taxa of *A. deliciosa* var. *deliciosa*, together with *A. deliciosa* var. *chlorocarpa*, all of which aggregate at a similarity level of 0.61.

Cluster "D" includes *A. latifolia*, three genotypes of *A. chinensis* var. *chinensis* and *A. eriantha*, as in Figures 5.5 and 5.6.

3.3.2.4 *Cluster analysis of the reduced data set using single-linkage*

Cluster analysis of the reduced data set by the method of single-linkage (Figure 3.8) generated subclusters "1" to "7" (numbered as previously) of nearly identical composition to those derived from the full set of O.T.Us (Figures 3.5, 3.6).

The five clusters derived from clustering by single-linkage, arise at a similarity level of 0.60, along with three of the O.T.Us as "outliers", namely *A. eriantha*, *A. indochinensis* and *A. callosa* var. *henryi*.

The most morphologically similar O.T.Us are *A. polygama* and *A. valvata* which unite at a similarity level of 0.70. The other O.T.Us form reasonably

compact groups over a range of 0.60 - 0.65 levels of similarity. Clusters "C" and "D" form a unified assemblage, which is more congruent with existing taxonomy (Liang 1984) than their position in Figure 3.7.

Table 3.7 Linkage Coefficients (U.P.G.M.A.)

OTU		Linkage Coefficient
9	POLYG3/12/9A	0.8783
10	VALV	0.8636
8	POLYG3/12/11	0.7424
5	RUFA	0.8491
16	HEMSLEY	0.8060
12	CHRYS	0.7725
15	MELL	0.7104
1	ARGARG	0.8544
3	ARGGIR	0.8462
4	ARGPURP	0.8045
2	ARGCORD	0.7989
6	MELAN	0.7655
7	KOLOM	0.6798
13	INDOCH36/3/11A	0.8367
14	INDOCH36/3/8B	0.6407
23	ADELGREENSILL	0.8719
26	ADELJONES	0.8668
22	ADELGRACIE	0.8450
27	ADELMONTY	0.8102
24	ADELALLISON	0.8580
25	ADELMATUA	0.8417
29	ADELCHLOROCARPA	0.8307
21	ADELABBOTT	0.8235
20	ADELBRUNO	0.7896
19	ADELHAY	0.8094
28	ADELELMWOOD	0.6540
18	LATIF	0.8455
30	ACHIN460/4	0.8122
32	ACHIN32	0.7951
31	ACHIN460/9	0.7209
17	ERIAN	0.5948
11	CALLHEN	0.0000

Cophenetic correlation = 0.746

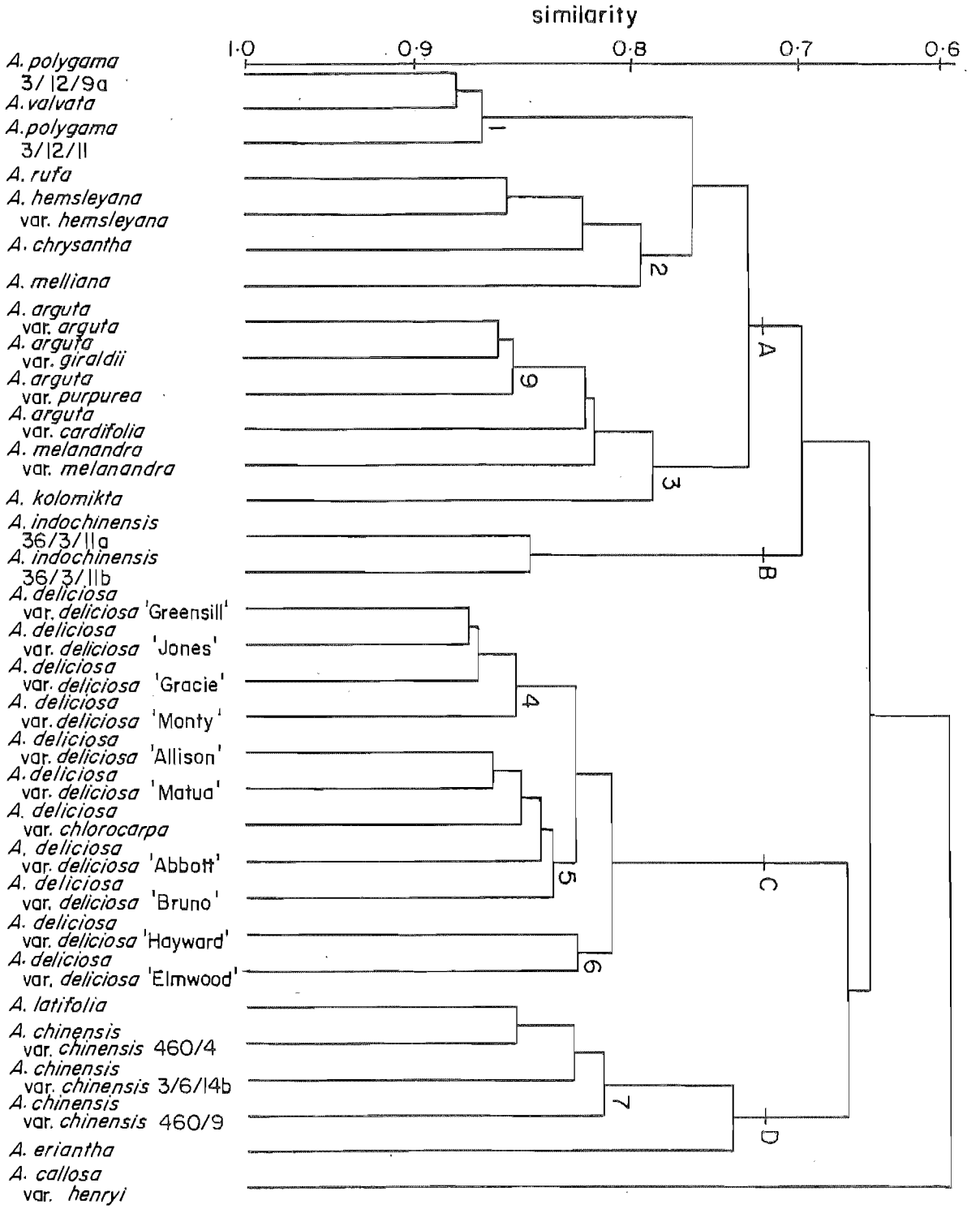


Figure 3·5: Cluster analysis of winter shoot characters using average-linkage

Table 3.8 Linkage Coefficients (Single)

OTU		Linkage Coefficient
9	POLYG3/12/9A	0.8783
10	VALV	0.8679
8	POLYG3/12/11	0.7898
5	RUFA	0.8491
16	HEMSLEY	0.8075
12	CHRYS	0.7903
1	ARGARG	0.8544
3	ARGGIR	0.8490
4	ARGPURP	0.8290
2	ARGCORD	0.8165
6	MELAN	0.8015
7	KOLOM	0.7897
15	MELL	0.7840
18	LATIF	0.8455
30	ACHIN460/4	0.8239
32	ACHIN32	0.8099
31	ACHIN460/9	0.7780
24	ADELALLISON	0.8580
25	ADELMATUA	0.8464
29	ADELCHLOROCARPA	0.8418
21	ADELABBOTT	0.8324
23	ADELGREENSILL	0.8719
26	ADELJONES	0.8672
22	ADELGRACIE	0.8489
27	ADELMONTY	0.8387
20	ADELBRUNO	0.8321
28	ADELELMWOOD	0.8195
19	ADELHAY	0.7710
13	INDOCH36/3/11A	0.8367
14	INDOCH36/3/8B	0.7644
17	ERIAN	0.7630
11	CALLHEN	0.0000

Cophenetic correlation = 0.693

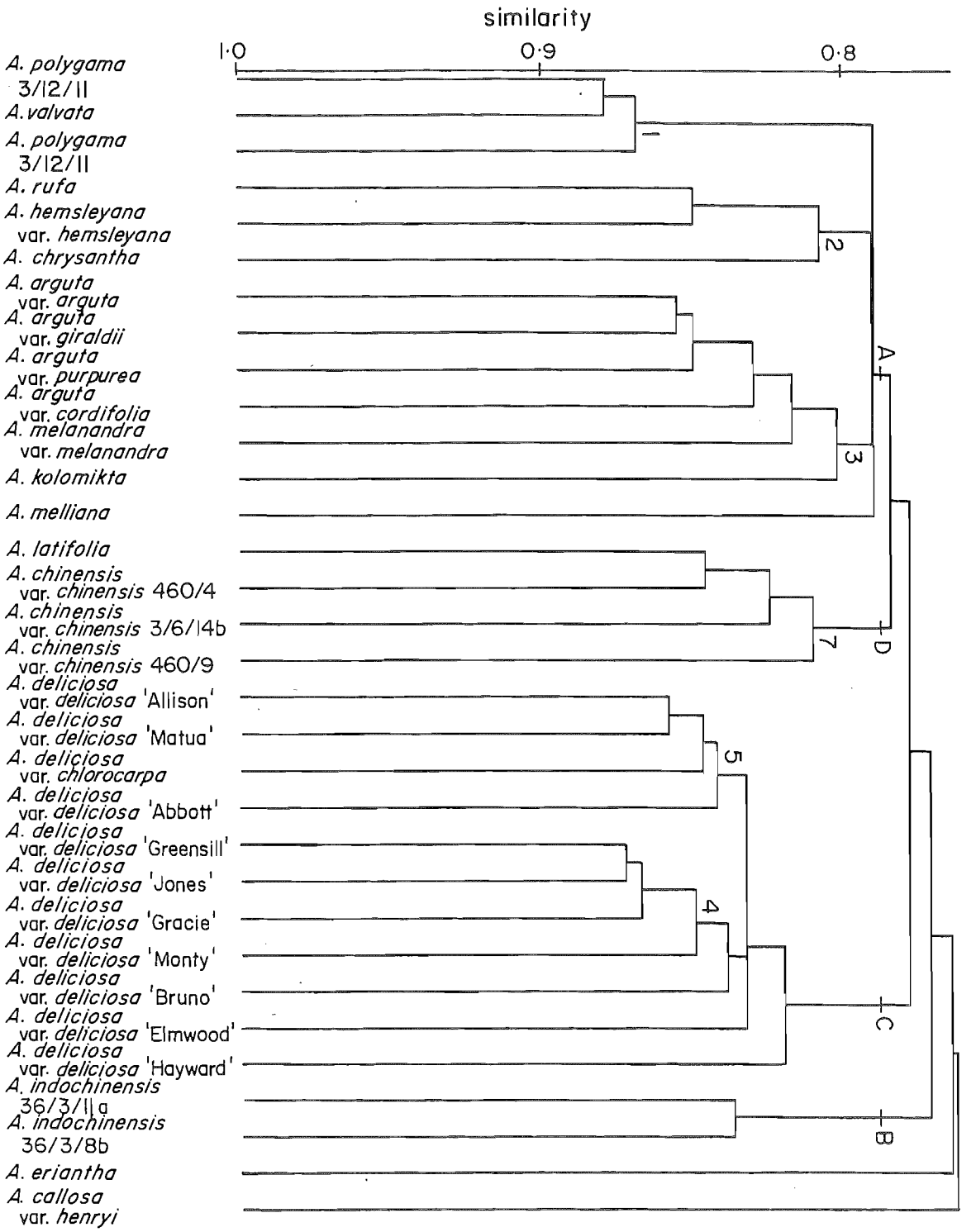


Figure 3·6: Cluster analysis of winter shoot characters using single-linkage

Table 3.9 Linkage coefficients reduced matrix (average)

	OTU	Linkage Coefficient
6	POLYG3/12/11	0.6974
7	VALV	0.5627
1	ARGARG	0.6608
5	KOLOM	0.6282
2	ARGCORD	0.6443
4	MELAN	0.5438
3	RUFA	0.6445
12	HEMSLEY	0.6150
9	CHRYS	0.6026
11	MELL	0.5065
17	ADELMATUA	0.6462
18	ADELCHLOROCARPA	0.6218
16	ADELBRUNO	0.6034
15	ADELHAY	0.4672
14	LATIF	0.6433
19	ACHIN460/4	0.6184
21	ACHIN32	0.6132
20	ACHIN460/9	0.5227
13	ERIAN	0.4565
8	CALLHEN	0.5110
10	INDOCH36/3/8B	0.0000

Cophenetic correlation = 0.722

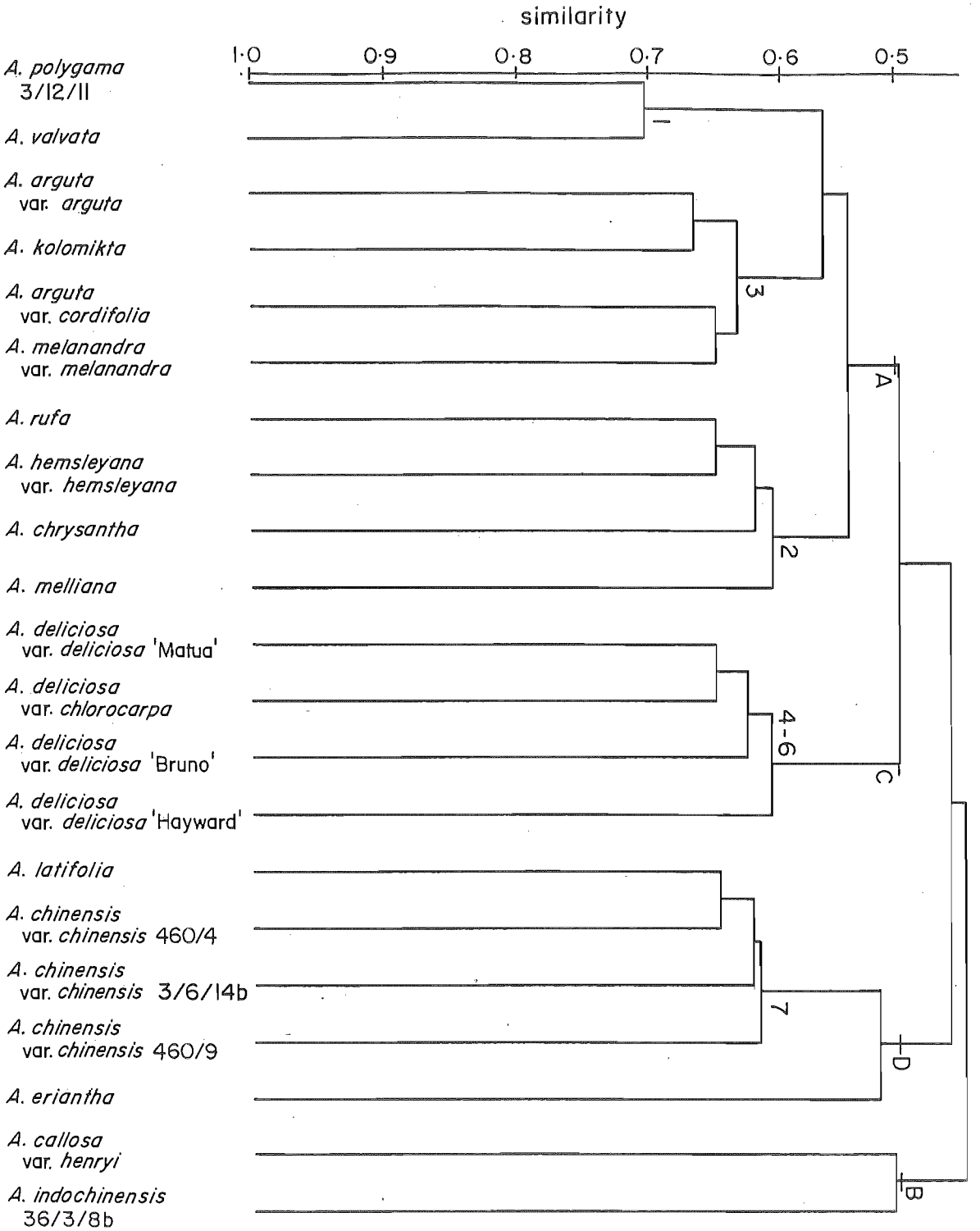


Figure 3·7: Cluster analysis of winter shoot characters (reduced matrix) using average - linkage

Table 3.10 Linkage coefficient reduced matrix (single)

	OTU	Linkage coefficient
6	POLYG3/12/11	0.6974
7	VALV	0.5953
1	ARGARG	0.6608
5	KOLOM	0.6552
4	MELAN	0.6504
2	ARGCORD	0.6110
3	RUFA	0.6445
12	HEMSLEY	0.6241
9	CHRYS	0.6144
11	MELL	0.5866
14	LATIF	0.6433
19	ACHIN460/4	0.6348
20	ACHIN460/9	0.6222
21	ACHIN32	0.5930
17	ADELMATUA	0.6462
18	ADELCHLOROCARPA	0.6237
16	ADELBRUNO	0.6204
15	ADELHAY	0.5670
13	ERIAN	0.5604
10	INDOCH36/3/8B	0.5595
8	CALLHEN	0.0000

Cophenetic correlation = 0.629

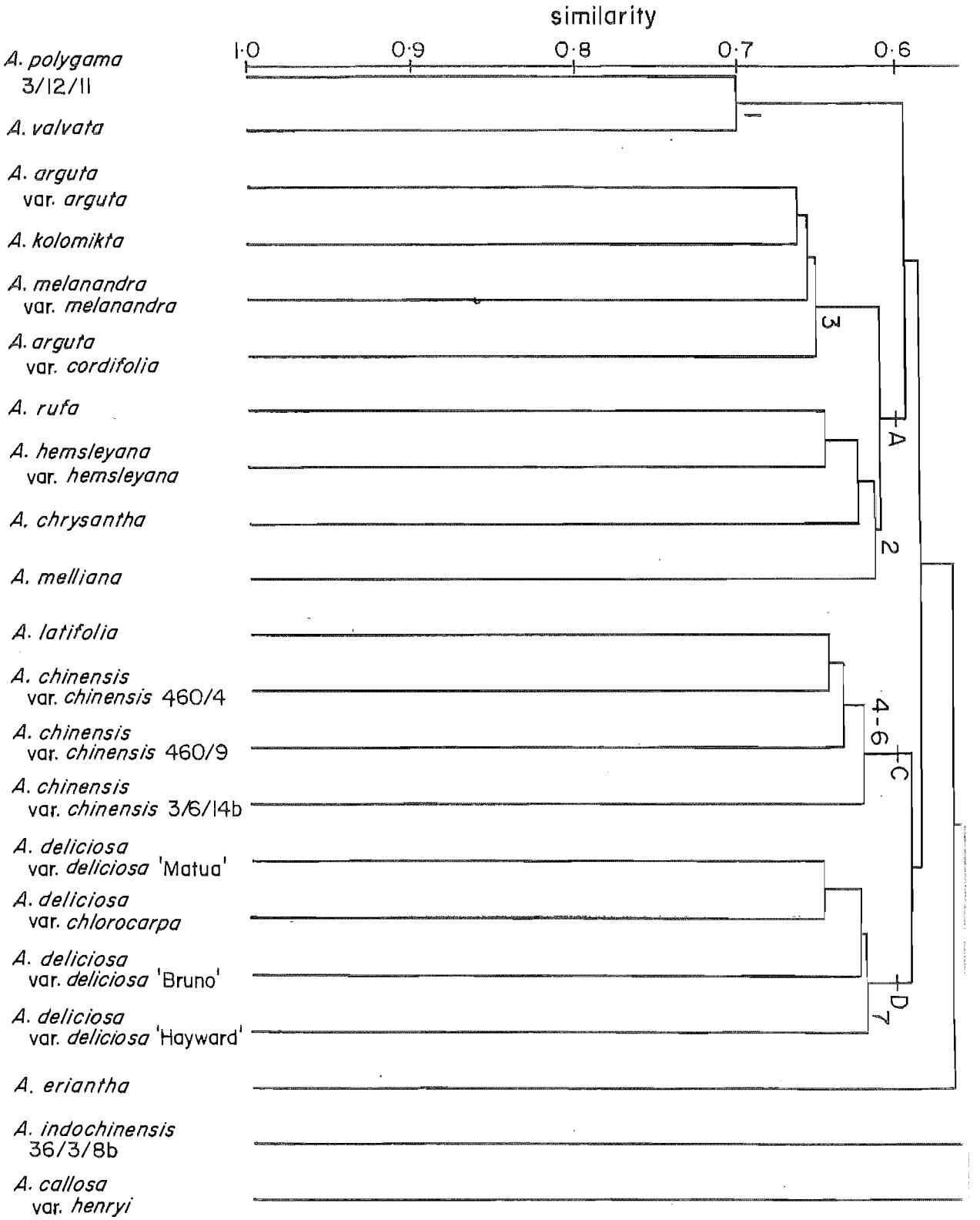


Figure 3·8: Cluster analysis of winter shoot characters (reduced matrix) using single-linkage

3.3.3 Discriminant analysis of winter shoot characters

Discriminant analysis (D.A.) is used firstly to validate the groupings derived from cluster analysis and secondly, to test the "discriminant efficacy" of selected characters relative to one another.

3.3.3.1 *Validation of the "a priori" groupings*

Cluster analysis of winter shoot characters by the method of average-linkage (Figure 3.5) generated four major groups (clusters "A" to "D"), which were geographically and/or taxonomically explicable. D.A. is used to test the hypothesis that the four *a priori* groups from cluster analysis are indeed valid. *A. callosa* var. *henryi* and both *A. indochinensis* genotypes, which clustered at a low similarity level, are transferred to discriminant group 4, together with subclusters "1" and "2" of cluster "A" (Figure 3.5). It is felt that these "outliers" in the phenogram result from distortions produced by the clustering procedure.

A. callosa var. *henryi* is the only O.T.U. with three winter shoots per bud; both *indochinensis* genotypes are very similar to one another, against the low level of similarity level for members of the same taxonomic group, i.e. the group itself may not be well-defined.

Results of the group validation procedure are presented in Table 3.11. This procedure reveals four groups in the multivariate data set, as I had hoped. These groups contain the same number of members as those groups predicted from our hypothesis, i.e. the four *a priori* groups generated from cluster analysis.

Table 3.11 **Group Validation by D.A.**

Gps	1	2	3	4	Totals
1	5	0	0	0	5
2	0	11	0	0	11
3	0	0	6	0	6
4	0	0	0	10	10
Totals	5	11	6	10	

Notes

1. Columns show the four predicted groups
2. Rows show groups detected by D.A.
3. Totals show number of members for predicted or detected groups.

Canonical variates analysis enables an ordination diagram (Figure 3.9) to be constructed from the major characters or character combinations, which polarise the four *a priori* groups (Figure 3.9). The first axis (termed "canonical variable 1") separates discriminant group 2 from the other groups, whereas the second axis

("canonical variable 2") further distinguishes groups 1 and 3 from the other groups. Clearly this validates the composition of the major groupings derived from average-linkage clustering (Figure 3.5). The major groups arising from D.A. can be identified as follows :

Groups
1. "lowland *Stellatae*"
2. *A. deliciosa* cvs = "highland *Stellatae*"
3. "highland *Leiocarpae*"
4. "*Maculatae-Strigosae* assemblage"

Group 4 is more "loosely-defined" than the other three groups. *A. polygama* (= O.T.U'S 9; 10), *A. hemsleyana* (= O.T.U. 16) and *A. rufa* (= O.T.U. 5) are among the more distinctive (spatially polarised) elements of this group.

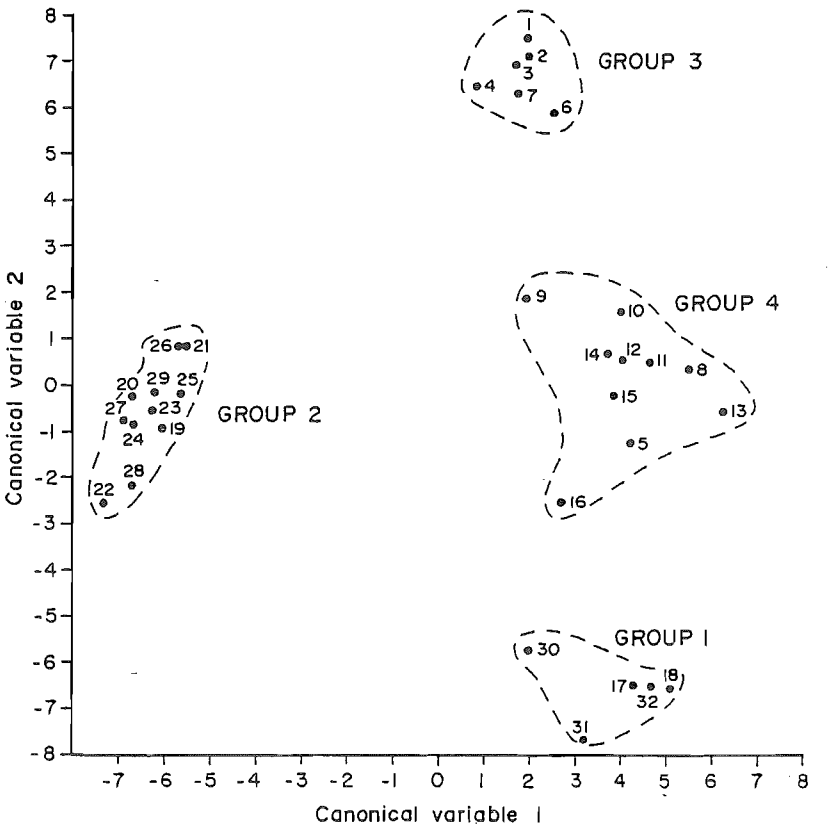


Figure 3·9 : Plot of canonical variable 1 against canonical variable 2 for the four species groups

GRAPHS OF MEANS ± 95% CONFIDENCE LIMITS, KEY TO TAXA CODES

Leiocarpae: 1 = *A. arguta var. arguta* 2 = *A. arguta* var. *cordifolia* 3 = *A. arguta* var. *giraldi* 4 = *A. arguta* var. *purpurea* 5 = *A. rufa* 6 = *A. melanandra* var. *melanandra* 7 = *A. kolomikta* 8 = *A. polygama 3/12/11* 9 = *A. polygama 3/12/9a* 10 = *A. valvata*

Maculatae: 11 = *A. callosa* var. *henyri* 12 = *A. chrysantha* 13 = *A. indochinensis 36/3/11b* 14 = *A. indochinensis 36/3/8b*

Strigosae: 15 = *A. melliana* 16 = *A. hemsleyana*

Stellatae: 17 = *A. eriantha* 18 = *A. latifolia* 19 = *A. deliciosa* 'Hayward' 20 = *A. del.* 'Bruno' 21 = *A. del.* 'Abbott' 22 = *A. del.* 'Gracie' 23 = *A. del.* 'Greensill, constricted' 24 = *A. del.* 'Allison' 25 = *A. del.* 'Matua' 26 = *A. del.* 'Jones' 27 = *A. del.* 'Monty' 28 = *A. del.* 'Elmwood' 29 = *A. del.* var. *chlorocarpa* 30 = *A. chinensis* var. *chinensis* 460/4 31 = *A. chinensis* var. *chinensis 3/6/14b* 32 = *A. chinensis* var. *chinensis* 460/9.

3.3.3.2 *Discriminant efficacy of winter shoot characters*

Discriminant analysis can be used to quantify the "discriminant efficacy", or the extent to which characters may separate the groups. Normally D.A. is restricted to the analysis of continuous characters, since discriminant efficacy is assessed by comparing the variance of characters between groups in relation to the background of variation within groups. Binomial or multistate continuous characters are normally inadmissible in D.A. because they do not generate any variance. D.A. of winter shoot characters is performed on the data matrix used for cluster analysis (Appendix 3.1), with the removal of characters 22 and 23 (stem colour and no. of shoots per bud case) for the reasons stated above.

The discriminant efficacy of the characters is ranked in descending order using results derived from a separate analysis of variance for each character considered in turn (Table 3.12). The character "ostiole-width" separates the groups most effectively, whereas, the character "longest lenticel" gives the worst separation of groups. The last six characters do not attain statistical significance, because the background of variation within groups, is greater than or equal to that between groups, i.e. these characters do not separate the groups.

Canonical variates analysis is performed in reverse to that of Figure 3.9, this time to show the spatial separation of characters rather than that of the O.T.U's (Table 3.12). Inspection of the tabulated figures for the first and second axes (canonical variates) show that "ostiole width", "ostiole length", "bud height" and "height of visible bud structures" are the characters which are mostly responsible for separating the groups. The first and second canonical coefficients account for 98.0 and 97.3% of the variation in the data set with these big values, indicating that lots of highly correlated characters are present.

A very simple means of visualising how that the characters separate the groups is shown in Figure 3.10. Eight of the most effective discriminating characters (those with the highest univariate F values) are presented as means for the four *a priori* groups (Figure 3.10), derived initially from cluster analysis (Figure 3.5). The best character "ostiole width" separates the four groups strongly from one another, whereas, the character "bud case height" only separates the pairs of groups "1" and "2" from "3" and "4". The bud heights of groups "1" and "2" are not statistically separable (not significantly different). The ratio of "bud-case height to cane diameter" - "BCCD" barely separates the four groups (Table 3.12; Figure 3.10).

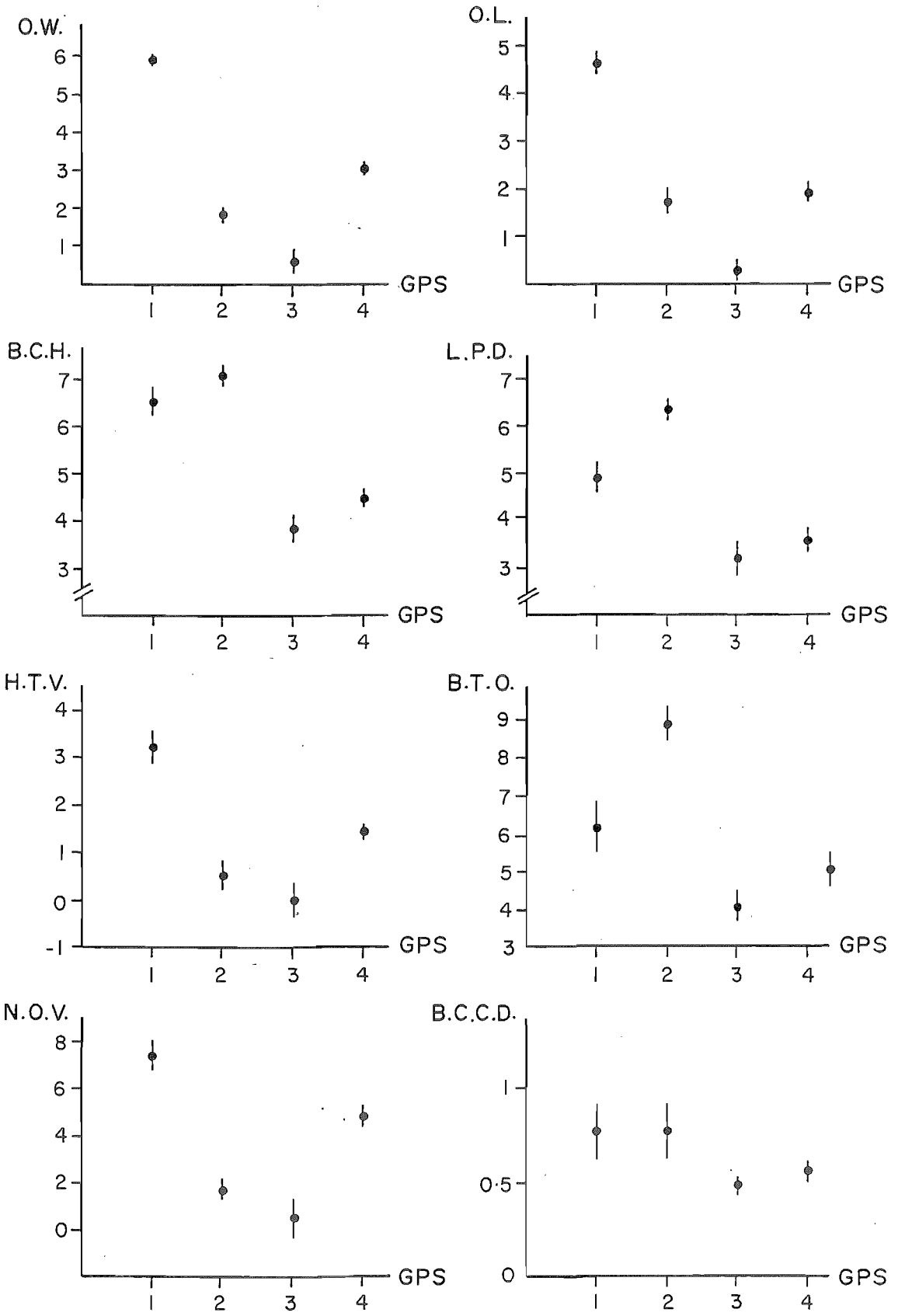


Figure 3·10: Means (± S.E.) of selected variables for the four groups

Table 3.12 **Statistics summarising "discriminant efficacy" of winter shoot characters**

Variable or "character"		Univariate $F^{1,2}$ value	First canonical coefft.std[3]	Second canonical coefft.std[3]
Ostiole width	(O.W.)	42.961	2.242	- 0.224
Ostiole length	(O.L.)	42.423	- 1.449	- 2.071
Bud-case height	(B.C.H.)	41.328	- 2.040	- 1.331
Longest petiole diameter	(L.P.D.)	39.224	0.420	0.613
Height of visible bud structures	(H.T.V.)	23.247	1.139	2.315
Bud-case : ostiole width	(B.C.O.W.)	18.686	0.841	0.146
Base to highest point of bud-case	(B.T.O.H.)	17.593	- 0.677	0.209
Number of visible bud structures	(N.O.V.)	16.957	- 0.871	- 1.120
Bud-case : cane diameter	(B.C.C.D.)	13.417	0.267	1.302
Bud-case width	(B.C.W.)	13.320	0.322	- 0.521
Bud-case length	(BUD.C.)	10.063	- 0.004	- 0.070
Bud-case height : bud-case length	(B.T.B.L.)	3.683	1.280	0.307
Depth of petiole scar	(D.PET.)	3.494	- 0.966	- 1.213
Longest lenticel	(L.E.N.L.)	2.975	0.370	- 0.578
Cane diameter	(C.D.)	2.776 n.s.	0.205	1.361
Bud-case length : bud-case height	(B.L.B.H.)	2.252 n.s.	- 0.650	- 0.260
Cane hair density	(CAN.H.)	2.218 n.s.	0.801	0.347
Number of externally visible bud structs : OW	(N.V.O.W.)	1.505 n.s.	0.318	0.334
Lenticel frequency side of bud-case	(LEN.F.)	1.450 n.s.	- 0.044	0.213
Depth of petiole scar : bud-case height	(D.P.B.H.)	0.227 n.s.	0.592	0.091

Footnotes :

1. F value = Ratio of variance of means among groups divided variances within groups.
2. Degrees of freedom: among gps = 3, within gps = 28 n.s. = not statistically significant $p > 0.05$.
3. Std on the basis of standard deviations within groups.
4. Std = standardised.

3.3.4 Internal bud structures of some *Actinidia*

3.3.4.1 *Types of bud structures*

The organisation of protective structures in *Actinidia* buds is as varied as the distribution of the taxa themselves. All buds have a semi-woody, suberised bud-case, which originates as an emergence from the stem cortex (Feist 1887, Hildebrand 1883, Lubbock 1899). The outer layer of the bud-case is thought to comprise a pair of fused stipules (Lionakis and Schwabe 1984a).

The dormant winter shoot may be small, compact and well sunken within the mass of cortical protective tissue, as in buds of *A. kolomikta* and *A. arguta* var. *arguta* (Plate 3.1), or to a lesser extent, in the *Leiocarpae* in general.

Buds of *A. deliciosa* do not protrude above the ostiole markedly, in contrast to other more lowland Stellatae, such as *A. latifolia* and many forms (ecotypes) of *A. chinensis* (Plate 3.3; 3.4).

Semi-deciduous or evergreen plants such as *A. indochinensis* of the *Strigosae* have exposed winter shoots, which burst early (during winter months (Ferguson 1990a), rather than enter into dormancy (Plate 3.2E,F)).

Recognition of bud structures in *Actinidia* is based on Brundell (1975a) and on observations derived from the present work (Plate 3.6).

Bud structures in *Actinidia* are mainly variations of entire leaves rather than stipules or modified leaf bases (Lubbock 1899). Buds of *A. deliciosa* have the full complement of structures from true leaves nearest the apex, through to a gradual transition of modified leaves with ligneous tips and culminating in mostly fully lignified scales, nearest the ostiole. Other *Actinidia* are more variable in their complements of bud structures and in their extent of lignification or pubescence (Plate 3.6).

Scales (Plate 3.5 D,E) are the outermost 3-4 leaf structures (nearest the ostiole), which are extensively lignified for $\geqslant \frac{3}{4}$ of the whole leaf area. They are brown to black or grey, they are usually glabrate and brittle to woody in texture. Scales may be fused at their bases nearest the stem.

Transitional leaves (Plate 3.5 B,C) are intermediary in character between scales and true leaves. They range from otherwise normal leaves which are progressively lignified for up to $\frac{1}{2}$ their length. The outermost transitional leaves may change in shape from ovate to elongate (see also drawings in Brundell 1975a).

True leaves (Plate 3.5) are easily recognised as fully herbaceous bud structures without ligneous pigmentation or modified apices. They are fleshy to soft in texture with leaf venation often obvious in older leaves. True leaves represent the earliest stages of the next season's canes, that is, 16-20 leaves prior to the inception of growth and internodal expansion in the following spring. True

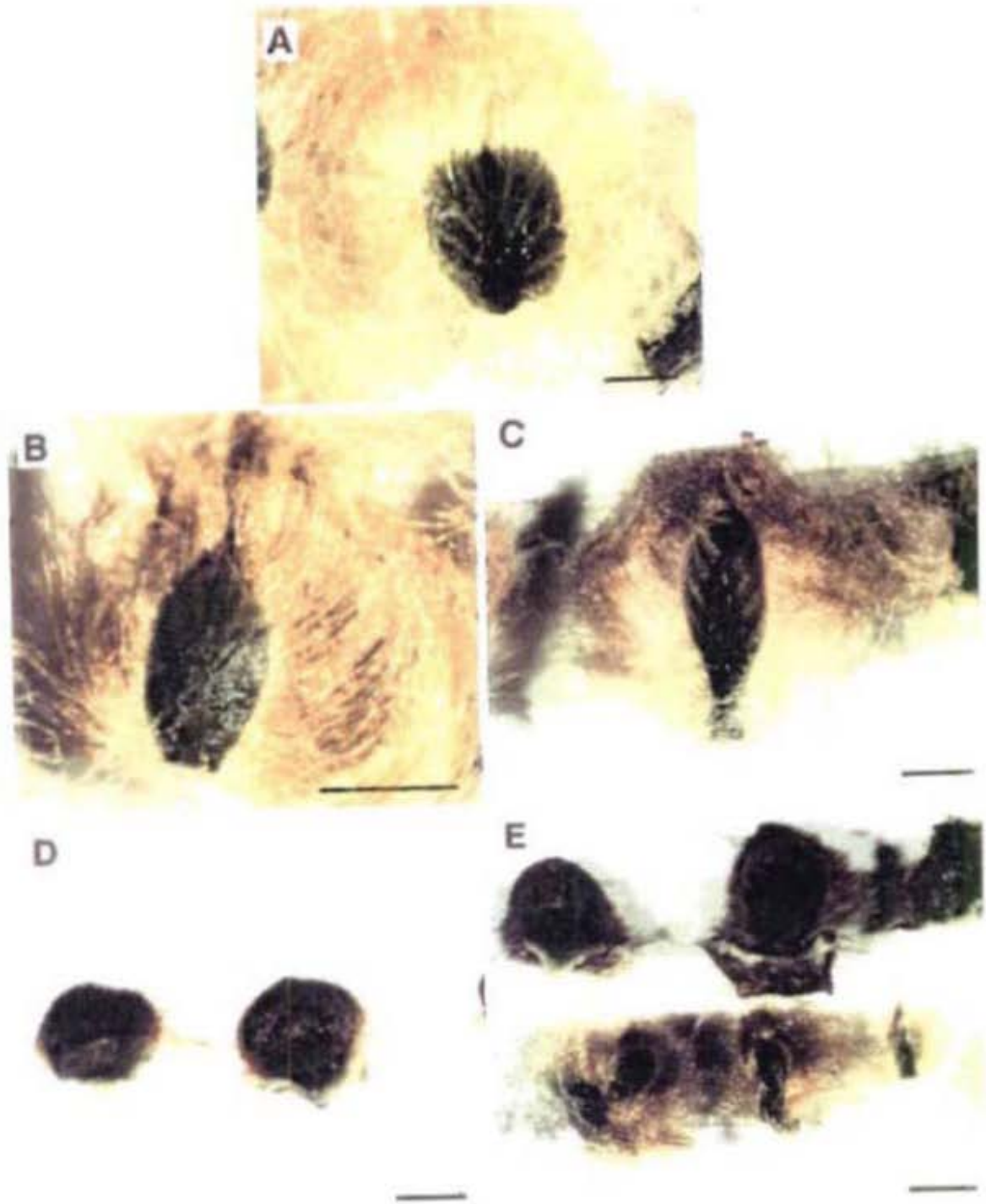


PLATE 3.5

Types of bud structures in dissected winter buds of some *Actinidia*.

A True leaf of *A. deliciosa* var. *deliciosa* cv. Elmwood.

B, C Transitional leaves of *A. deliciosa* var. *deliciosa* cv. Abbott and *A. eriantha*, respectively.

D, E Ligneous scales of *A. chrysantha* and *A. indochinensis*, respectively.

Bar scale = 1 mm

leaves exhibit a greater range of developmental stages than other bud structures as they include "unfurled" leaves and leaf primordia of the apical dome.

In practice, it may be difficult to assign bud structures to one or other of these categories, as the transition between the various types of bud structures is gradual in most *Actinidia.*

3.3.4.2 *Bud structure complements of selected Actinidia*

Stereo-microscopic dissections of the 32 *Actinidia* studied from the kiwifruit germplasm collection, reveal 4 groupings of bud structure complements (Plate 3.6) :

"GpI"	-	small ostioles
	-	thin leaves
	-	mostly glabrate, but for sparse adaxial hairs
	-	partial complement of bud structure types, i.e. scales rare or absent (includes *Leiocarpae*)
"GPIIA"	-	small ostioles
	-	thick fleshy leaves
	-	dense lanate hairs *ca.* 1-2 mm long
	-	full complement of bud structure types, i.e. 3-4 scales, modified leaves; true leaves (includes "Mountain *Stellatae*", various taxa of *A. deliciosa*)
"GpIIB"	-	large ostioles
	-	thick fleshy leaves
	-	dense lanate hairs *ca.* 1-2 mm long
	-	full complement of bud structure types (includes "Lowland *Stellatae*", *A. rufa* and *A. melliana*)
"GpIII"	-	large ostioles
	-	thick fleshy leaves
	-	dense strigose, short to medium hairs ca. 0.5-1.0 mm long
	-	full complement of bud structure types (includes *Maculatae-Strigosae*)

Bud dissections reveal distinctive colours in the leaf hairs prior to bud-break in the spring, e.g. *A. callosa* var. *henryi*, *A. indochinensis*, *A. kolomikta* and *A. arguta* in part, have reddish, speckled and colourless hairs ca. 0.1-0.3 mm long. In other buds the hairs are more ochre in colour, e.g. *A. valvata*, *A. rufa*; *A. latifolia* and *A. chinensis* var. *chinensis*. The internal hairs of true leaves in *A. deliciosa* buds are described in Brundell (1975a). The sporadic hairs on the upper surface of mature leaves of *Leiocarpae* sampled are apparent on leaves within the winter bud.

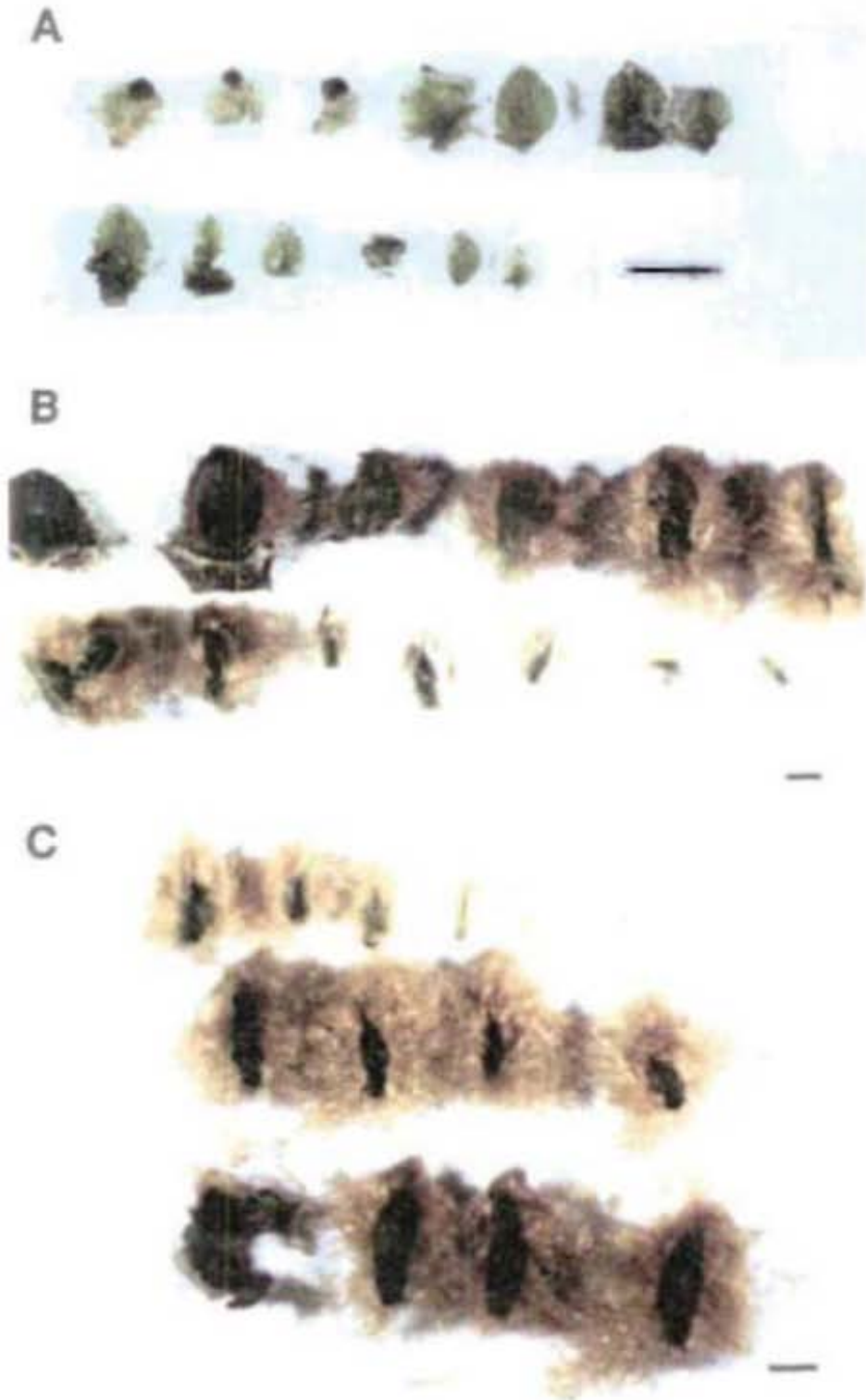


PLATE 3.6:

Bud structure complements from dissected winter buds of some *Actinidia*.

A *A. kolomikta*, "Gp I".
B *A. callosa* var. *henryi*, "Gp II B".
C *A. deliciosa* var. *deliciosa* cv. Gracie, "Gp III".

Bar scale = 1 mm

Observations of glasshouse grown *A. deliciosa* plants shortly after bud-burst (25 September 1989), reveal the persistence of spathulate transitional leaves whose lignified tips are intact. Only rarely are scale-like structures observed at advanced stages of bud-burst and then solely on acropetal buds. Abscission of scales and transitional leaves proceeds centripetally, so that true leaves are the only structures to grow and persist on the current year's shoot.

3.3.5 Infraspecific variation in selected genotypes of *A. chinensis* var. *chinensis*

The D.S.I.R. Kiwifruit germplasm collection includes several genotypes of *A. chinensis* var. *chinensis*, obtained from various provinces in China, ranging from coastal lowland to inland mountainous regions (Table 3.2). *A. chinensis* is the most polymorphic and widely distributed of any *Actinidia* species (Liang 1975, 1983). Infraspecific variation of this nature facilitates the use of selected ecological genotypes (ecotypes) in breeding experiments, so that climatic tolerances and chilling requirements of existing cultivars might be altered through artificial hybridisation.

3.3.5.1 *Descriptive trends in genotypes*

Stem colour is variable within and between genotypes of *A. chinensis* (Table 3.13). Some of this variation arises from changes associated with "ripening" or lignification of the canes (Berestova 1970). Colour may also be influenced by exposure of canes to light, for example canes of *A. deliciosa* are often green on their undersides and red-purple where sunlit. Much of the variation expressed in the experimental orchard is probably genotypic in origin. Cane colours range from green-ochre to chocolate brown with fawn-ochre colouration of surfaces subjected to "windrub" (wind-induced abrasion).

Genotypes originally obtained from coastal provinces such as Guangxi (see Figure 3.1) and Jiangxi (Plate 3.7) have sparingly pubescent (puberulous) to glabrous canes, whereas those canes of plants from Hunan are noticeably asperous in texture, with longer more hispid hairs. Plants examined from Hunan have more persistent stem hairs and a greater proportion of the indument is "entire" in both buds and stems. Trichomes of plants from Jiangxi and Guangxi persist as stubble-like remains of hair bases at maturity, with basipetal vestiges of the emergent hairs remaining in some instances. The more puberulous canes have a small percentage of intact hairs proximal to the bud-case.

Lenticels are consistently ovoid or elongate in form and are variously pigmented, with darkly coloured orange to brown centres, which are in turn surrounded by white, grey, cream or fawn coloured "edges", depending on the particular genotype. Most canes have raised to protuberant lenticels, but in some cases, the lenticels are obviously protuberant, becoming ruptured on occasion, e.g. G3C3, G2A4.

3.3.5.2 *Remarks on specific genotypes*

Some characters are relatively invariant within this taxon; these are mainly bud-shape characters such as bud-case length and bud-case height (Table 3.14). Departures in these apparently stable characters are viewed as significant. Two genotypes in this study are reminiscent of *A. deliciosa* (G4B3 from Guangxi and G4D2 from Jiangxi), in that they have much longer buds, with larger petiole diameters (L.P.D) and somewhat concealed bud structures (Plate 3.7).

Genotypes originating from colder regions, (e.g. Hunan; see Figure 3.2 map; remarks in Blanchet 1989) have narrow, shallow buds with smaller ostioles and reduced petiole diameters. The smaller petiole diameters may be related to slower rates of growth of petioles and their subtending leaves, which may indicate less favourable growing conditions. There is also some indication that *A. chinensis* genotypes from colder localities such as Lushan mountain ca. 5000 ft in altitude, have a greater number of heavily lignified winter shoot structures than those obtained from milder regions (Plate 3.8).

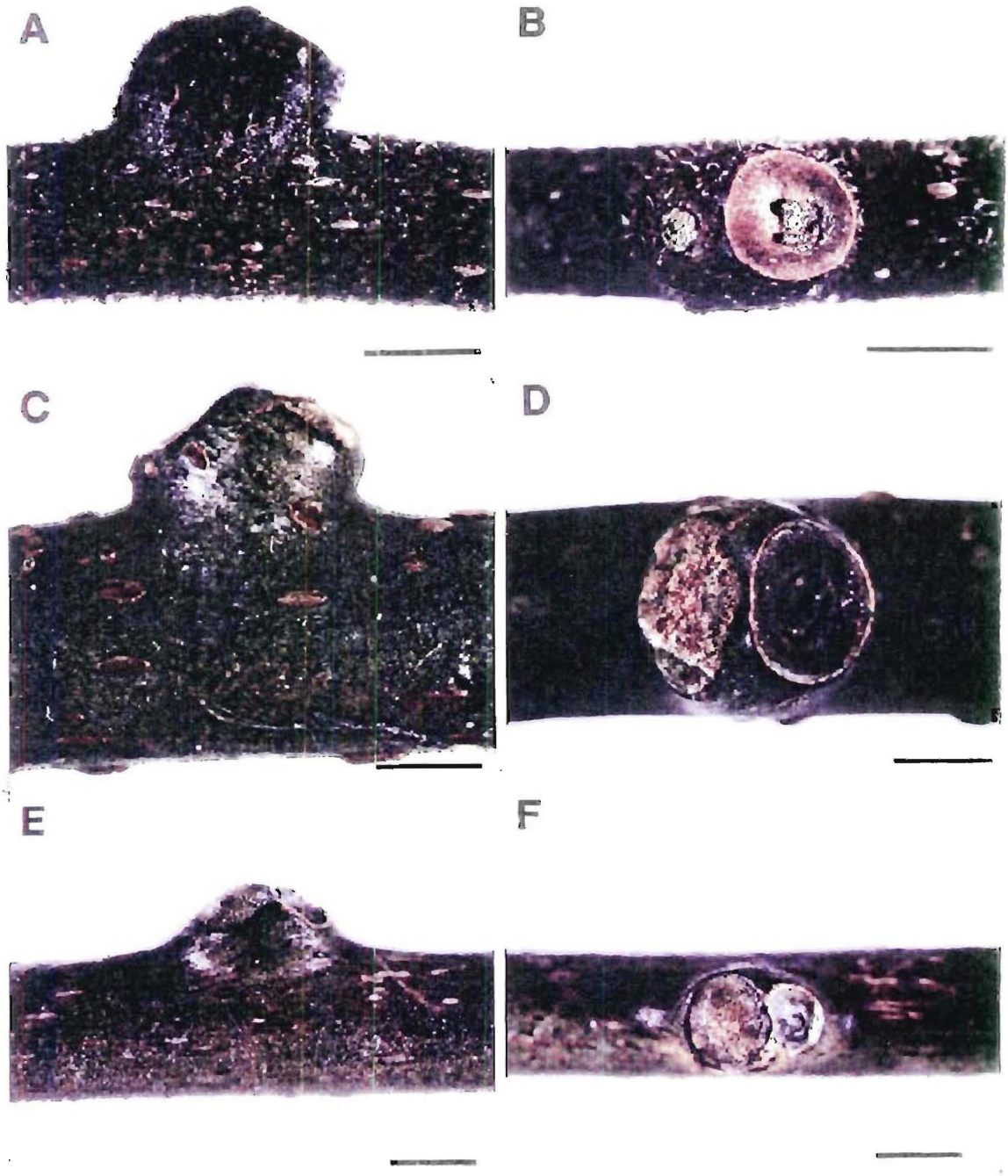


PLATE 3.7:

Profile and plan views of outer bud-cases of selected genotypes of *A. chinensis* var. *chinensis*.

A,B CN15, G4B3 from Guangxi "delicioid" bud form

C,D CN14, G4H1 from Guangxi "warm climate" form

E,F CN17, G4D2 from Jiangxi "cool climate" form

Bar scale = 5 mm

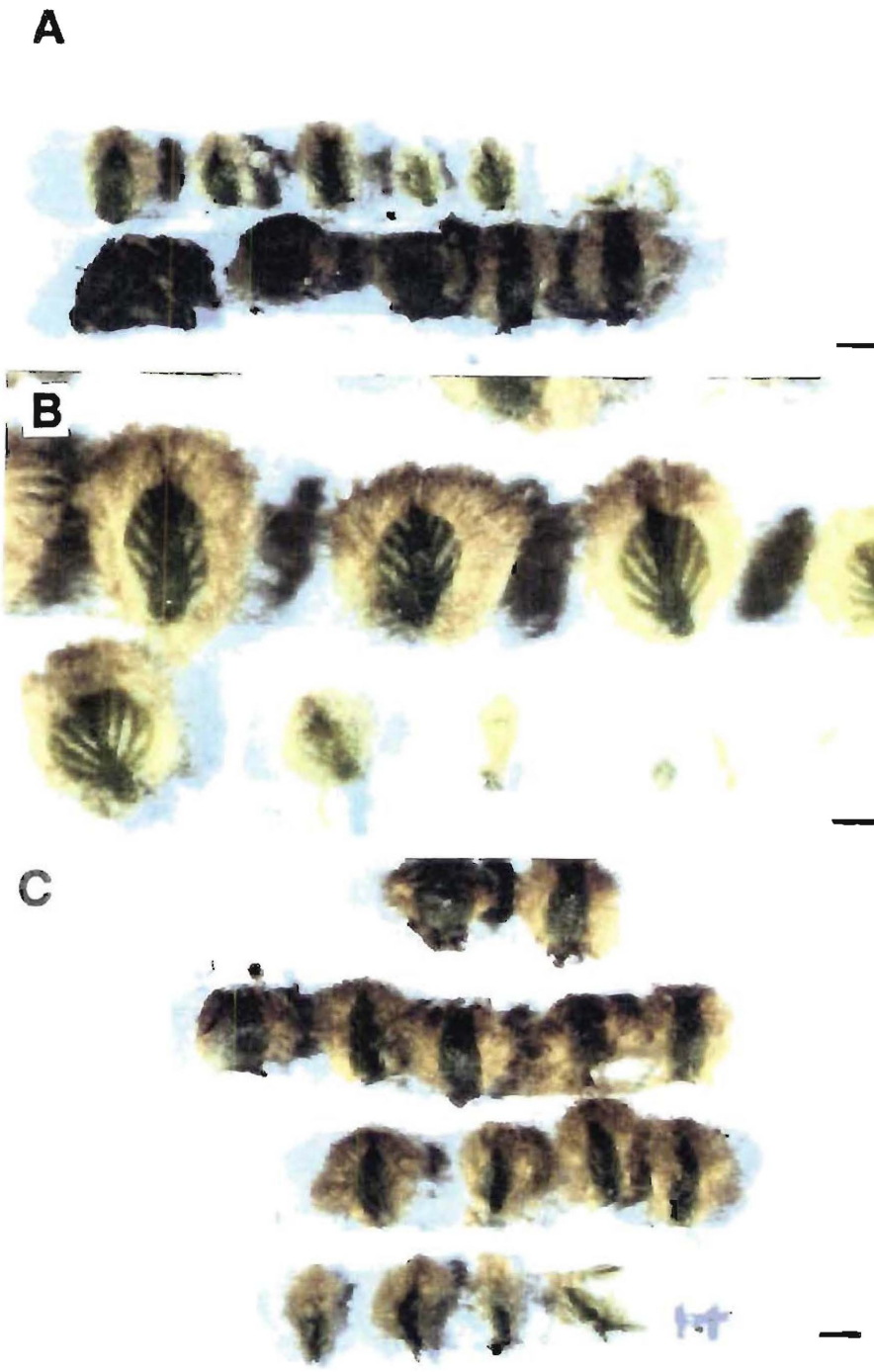


PLATE 3.8:

Dissections of selected genotypes of winter buds of *A. chinensis* var. *chinensis*.

A CN12, F4B5 from Hunan ("cool climate")
B CN15, G4D5 from Jiangxi ("cool climate")
C CN15, G4B3 from Jiangxi ("warm-temperate")

Bar scale = 1 mm

Table 3.13(a) Bud descriptions of some *A. chinensis* var. *chinensis* genotypes

Chinese province of origin Genotype	designation	Cane colour	Stem (cane) Texture	Gloss	Stem hair Quality	Colour
Guangxi CN14	G4H5	pale chocolate-brown, green-ochre undersides	smooth polished	glossy	apparently glabrous	N.A.
Guangxi CN14	F4I5	very dark green to brown	smooth	glossy	virtually glabrous at maturity	N.A.
Guangxi CN14	G4H1	greenish to slightly glaucous	smooth polished	glossy	virtually glabrous at maturity	N.A.
Guangxi CN15	G4B3	dark brown to greenish brown younger more ochre	finely furry	matt	finely tomentose soft hairy	orange to brow
Guangxi CN15	G4B4	chocolate-brown to green-brown, greenish undersides	finely furry		Finely tomentose soft hairy	white to orange-brown
Guangxi CN15	G4B5	brown to greenish ochre undersides	finely furry	matt	finely tomentose soft hairy	pale orange-brown
Hunan CN12	F4B5	red-purple to chocolate-brown, younger green-ochre	rough asperous		hispid, stiff	orange-brown
Hunan CN12	G2A4	green-ochre to chocolate-brown	rough asperous		hispid, stiff	white to orange brown
Hunan CN12	G3A5	greenish-ochre	rough asperous		hispid long hairs	cream-ochre
Hunan CN07	G2F3	green-brown to dark brown	rough asperous		hispid, stiff	orange-brown
Hunan CN07	G2D6	green-ochre to chocolate-brown	rough asperous		hispid, stiff	whitish
Hunan CN07	G2E6	dark green to chocolate-brown, ochre undersides	rough asperous		bristly stiff	white to orange-brown
Jiangxi CN03	G3C3	dark brown, fawn-ochre undersides	smooth	matt	virtually glabrous	N.A.
Jiangxi CN03	G3C1	dark green to brown fawn-ochre undersides	semi-smooth	matt	apparently glabrous	N.A.
Jiangxi CN03	G3C2	dark brown, green to fawn-ochre undersides	semi-smooth	matt	hispid	whitish-brown
Jiangxi CN17	G4D5	golden fawn, green-ochre hue	semi-smooth	matt	finely tomentose, virtually glabrous	N.A.
Jiangxi CN17	G4D2	greenish to greyish ochre-brown	semi-smooth	matt	finely tomentose, virtually glabrous	N.A.
Jiangxi CN17	G4D3	pale greenish brown with ochre to orange caste	matt to fluffy	pruinose	finely tomentose,	ochre to orange

Table 3.13(b) Bud descriptions of some *Actinidia* var. *chinensis* genotypes

Chinese province of origin Genotype	designation	Stem hair extent length	Lenticel colour	Lenticel shape	Lenticel protuberance
Guangxi CN14	G4H5	sporadic stubble on buds, bases or glabrous elsewhere	orange-brown centres, cream to white edges	mostly ovoid, less elongate	raised to protuberant
Guangxi CN14	F4I5	some entire near bud, general cover of bases elsewhere	brown-grey centres, orange to brown edges	mostly elongate and ovoid	lenticels not raised flat and elongate
Guangxi CN14	G4H1	general cover of minute hair bases	orange-brown centres, orange-brown edges	mostly elongate and ovoid	extremely protuberant
Guangxi CN15	G4B3	entire hairs on bud 2-3 mm, dense stubble elsewhere	orange-brown centres, cream-brown edges	much elongated few ovoid	raised to protuberant
Guangxi CN15	G4B4	general cover of entire hairs 1-2mm and long stubble	orange-brown centres, white-cream edges	mosty ovoid and elongate	not raised flat and elongated
Guangxi CN15	G4B5	mostly entire 2-3 mm, esp.near buds	orange-brown centres, white-cream edges	mostly ovoid and elongate	raised to protuberant
orange-brown Hunan CN12	F4B5	entire near bud, stubble or bases elsewhere	orange-brown centres, fawn-ochre edges	mostly ovoid and elongate	raised to protuberant
Hunan CN12	G2A4	entire on old canes 2-3 mm, stubble elsewhere	greyish centres, orange-brown edges	mostly ovoid and elongate	raised to very protuberant "lumpy"
Hunan CN12	G3A5	entire hairs 2-3 mm long, complete cover	pale orange-brown centres, grey edges	mostly ovoid and elongate	raised to protuberant
Hunan CN07	G2F3	entire near buds 2-3 mm, stubble ⩽ 0.5 mm elsewhere	orange-brown centres, white-cream edges	mostly ovoid and elongate	raised to protuberant
Hunan CN07	G2D6	entire hairs 2-3 mm, and long stubble	orange-brown centres, white-cream edges	mostly ovoid and elongate	raised to protuberant
Hunan CN07	G2E6	entire on bud 2-3 mm, stubble elsewhere	brownish centres, fawn-grey edges	mostly ovoid and elongate	raised to protuberant
Jiangxi CN03	G3C3	stubble or entire near bud 1-2 mm, Minute bases elsewhere	chocolate-brown centres, fawn-ochre edges	mostly spherical and ovoid, few elongate	protuberant "lumpy" to ruptured
Jiangxi CN03	G3C1	entire near bud, minute stubble or bases elsewhere	pale orange-brown centres, fawn-cream edges	mostly ovoid and elongate	protuberant obviously
Jiangxi CN03	G3C2	entire near bud 1-2 mm, bases common elsewhere	orange-brown centres, white-cream edges	mostly ovoid and elongate	protuberant obviously
Jiangxi CN17	G4D5	entire near bud 1-2 mm, bases common elsewhere	brown centres, cream-ochre edges	mostly ovoid and elongate	not obviously raised, very small
Jiangxi CN17	G4D2	general cover of minute hair bases	dark brown centres, green-white edges	mostly ovoid and elongate	raised to protuberant
Jiangxi CN17	G4D3	general cover of dense persistent stubble	dark brown centres, green-ochre edges	mostly ovoid and elongate	very raised to protuberant

Bud variables (Ranges) of some *A. chinensis* genotypes

Table 3.14

Chinese province of Origin / Genotype	designation	Bud-case length (mm)		Bud-case height (mm)		Bud-case width (mm)		Ostiole width (mm)		Number of structs visible through ostiole		Height of structs visible through ostiole (mm)		Cane lenticel density (cm^{-2})		Longest cane lenticel (mm)		Cane hair base density cm^{-2}		Petiole diameter on bud case (LPD) (mm	
Guangxi CN14	G4H5	7.80	13.00	4.50	7.50	6.50	9.50	7.60	12.50	9.00	12.00	3.20	4.60	8.00	14.00	1.10	4.50	144	1600	5.00	7.00
Guangxi CN14	F4I5	8.00	12.00	5.00	8.00	5.60	8.00	4.60	8.50	8.00	12.00	2.30	3.50	8.00	17.00	2.50	4.50	320	4800	5.50	7.00
Guangxi CN14	G4H1	8.00	13.00	7.00	10.00	7.00	10.50	7.20	10.50	8.00	15.00	2.50	8.00	3.00	12.00	1.50	4.00	1680	6400	5.50	7.50
Guangxi CN15	G4B3	12.00	20.00	5.00	8.50	6.00	8.00	6.00	7.80	9.00	14.00	2.20	3.60	5.00	24.00	3.80	20.00	160	1000	4.20	8.00
Guangxi CN15	G4B4	6.00	12.00	5.00	7.20	6.00	8.00	4.00	10.00	4.00	9.00	1.60	3.00	4.00	24.00	1.40	2.00	80	500	4.20	5.20
Guangxi CN15	G4B5	8.00	11.50	6.00	8.00	7.30	9.00	6.00	8.50	5.00	12.00	1.00	3.00	5.00	10.00	1.10	2.20	600	1300	4.60	6.20
Hunan CN12	F4B5	7.00	11.00	4.00	7.00	4.60	7.20	4.00	6.10	3.00	6.00	1.40	2.60	4.00	13.00	4.00	13.00	40	240	4.00	5.00
Hunan CN12	G2A4	9.00	15.00	6.00	8.00	4.60	7.20	4.00	7.00	6.00	12.00	2.00	5.10	8.00	60.00	1.20	3.00	40	400	4.00	6.00
Hunan CN12	G3A5	8.00	12.30	6.00	9.00	6.00	8.00	5.70	9.50	9.00	12.00	3.00	6.50	8.00	28.00	1.20	3.00	40	270	4.60	6.10
Hunan CN07	G2F3	8.00	10.00	5.00	9.00	5.50	7.00	3.60	6.00	6.00	12.00	3.00	4.60	12.00	52.00	2.20	5.70	40	200	4.00	6.00
Hunan CN07	G2D6	12.00	14.00	4.50	7.20	6.00	7.00	5.00	7.20	8.00	12.00	2.00	3.50	20.00	60.00	0.70	1.70	80	480	4.80	6.50
Hunan CN07	G2E6	8.00	12.00	6.00	8.00	4.80	7.50	4.80	8.10	10.00	12.00	3.00	5.00	8.00	24.00	2.00	4.00	38	200	4.80	6.50
Jiangxi CN03	G3C3	8.00	12.00	4.00	8.00	5.50	9.00	4.00	7.00	5.00	9.00	3.60	6.00	5.00	20.00	1.10	2.50	30	480	4.00	5.50
Jiangxi CN03	G3C1	8.00	12.00	7.50	9.00	7.00	9.50	7.00	9.00	7.00	9.00	3.00	5.00	5.00	16.00	1.60	2.50	60	400	4.30	6.00
Jiangxi CN03	G3C2	6.00	12.00	4.00	8.00	5.00	8.00	7.00	9.00	7.00	9.00	3.00	4.20	8.00	16.00	0.70	2.30	280	1600	4.00	6.00
Jiangxi CN17	G4D5	11.00	13.00	5.00	8.00	6.00	8.00	7.00	10.00	7.00	10.00	7.00	12.00	8.00	24.00	0.80	2.00	10	500	4.80	6.20
Jiangxi CN17	G4D2	12.00	16.00	4.00	6.00	5.50	7.00	8.00	12.00	8.00	12.00	1.20	2.80	6.00	15.00	1.20	2.80	20	1200	5.00	7.00
Jiangxi CN17	G4D3	9.00	13.00	6.00	7.50	6.00	8.00	9.00	11.00	9.00	11.00	2.20	4.00	9.00	20.00	1.20	2.00	800	1000	4.00	5.00

Table 3.14 continued....

3.4 DISCUSSION

The genus *Actinidia* is widely distributed across Asia, with plants ranging from Siberia in the north to Indonesia in the south, with a geographic centre of diversity located in S.W. China (Dunn 1911, Liang 1983). As kiwifruit has only been intensively domesticated in the last 30-40 years, many of the genetic resources of the parent species *A. deliciosa* are still available in the wild. However, many indigenous taxa are being destroyed during land clearance, or are being damaged by peasants harvesting fruit or firewood (Ferguson 1990a). It is therefore important to conserve and document as many of the genetic resources of the genus, while the plants are still available, both for "genetic renewal" of existing cultivars and for artificial creation of new cultivars in the future.

Comparative morphological studies can play a role in this process by documenting "economically-useful" and "non-adaptive" or idiosyncratic variation displayed by species and cultivars. This information can be used in breeding and identification of *Actinidia* in the future.

Plants of the N.Z. *Actinidia* germplasm collection have been assembled for breeding new *Actinidia* cultivars under experimental garden conditions. The present study offers the potential for documentation of genotypic variation in a way that is not possible for Chinese taxonomists, such as Liang (1984), collecting plants from the wild. Under the common experience of orchard cultivation involving an imposed management system and a common climatic regime, genotypic variation in *Actinidia* can be described and evaluated for its horticultural relevance and potential.

Most kiwifruit plantings in the world are clones of N.Z. cultivars, which probably originated from one of two importations of Chinese seed in 1897 and 1915 by a N.Z. missionary Miss Katie Fraser. Plant material was later distributed to nurserymen such as Bruno Just of Palmerston North and Hayward Wright of Auckland, who gave their names to selections such as 'Bruno' and the cultivated variety 'Hayward' which is now termed kiwifruit. Details of kiwifruit domestication are found in Ferguson and Bollard (1990).

Treatment of infraspecific variation is mostly limited to *A. deliciosa* and *A. chinensis*. This would be a serious objection if I were attempting to produce a monograph of the genus. Descriptions in this chapter, however, are intended to show how comparative morphology can be used as an aid to taxonomy and horticulture in *Actinidia*. The taxonomic potential of this data set is tested independently using multivariate methods such as cluster analysis. The morphological variation described in this chapter may not be fully representative

of *Actinidia* in the wild, but it is representative of the variation contained in the germplasm collection in N.Z.

3.4.1 Taxonomy

Horticulturists who might need to manipulate *Actinidia* in the winter cannot identify these plants from synopses in Liang (1984). In his general description of the genus, Liang mentioned winter buds only briefly but not elsewhere in the flora :

> .....winter buds embedded in or naked outside the swollen base of the petioles.
>
> *Flora Reipublicae Popularis Sinicae*, page 2.

This is somewhat surprising, since Liang (1982a) had previously confirmed that Planchon's type specimen of *A. chinensis* collected in 1847, was the soft-haired variety, var. *chinensis*, on the basis of its leaf size and bud form, to quote :

> He [Planchon] also described how the lateral branchlets have leaves which originate from a raised bud. This too is one of the soft-haired variety's distinguishing characteristics.
>
> Liang 1982a, page 103.

Gui (1981) noted that differences between the overwintering buds of var. *chinensis* and var. *hispida* were the most pronounced of the characteristics distinguishing these varieties, in that, the buds of var. *chinensis* were exposed, whereas, those of var. *hispida* were deeply hidden. Gui attributed these features to the different distributions of these taxa.

Ferguson (1990b) suggested that *A. chinensis* (var. *chinensis*) and *A. deliciosa* (syn. *A. chinensis* var. *hispida*; Liang and Ferguson 1984, 1986), could be distinguished on the basis of their buds :

> *A. chinensis* : Bud base is small. Bud is almost spherical, exposed, covered only by bud scales....
>
> *A. deliciosa* : Bud base is large and protruding. The bud is almost completely submerged in the bark with only a small aperture....
>
> Ferguson (1990b), page 9.

These descriptions agree with my observations presented in this chapter.

Poyarkova (1949) used bud protection characteristics his keys to Russian *Actinidia*, mostly of the *Leiocarpae* :

e.g. *A. kolomikta* had :

> buds completely concealed under a pad of bark above the leaf scar.

and *A. polygama* had :

> upper parts of buds exposed.

Poyarkova 1949, page 140.

It is unfortunate that Liang (1984) did not describe his plants with the thoroughness of previous authors. This may have been because he relied too heavily on herbarium specimens, in which bud characters become obscured during pressing and drying.

Buds of *Leiocarpae* grown in New Zealand are morphologically similar to those of Russian plants. Chinese descriptions of *A. deliciosa* and *A. chinensis* buds are also in agreement with plants grown in N.Z. Winter buds of our N.Z. plants are therefore taxonomically, if not statistically, representative of geographic extremes of the genus *Actinidia*. Buds of *Maculatae* and *Strigosae* are not described in the literature, so no comparisons can be made with plants of the germplasm collection.

3.4.1.1 *Stem surface characters*

The surface of the stem yielded many characters for identifying the plants. Care was needed in differentiating between phenotypic and genotypic components of stem colour. The surfaces of canes subjected to "wind-rub" were often lighter in colour than the rest of the cane. The shaded undersides of canes were also less pigmented, indicating a possible role of photo-oxidation in the development of stem (cane) colour. It would be useful to investigate the possible chemotaxonomic basis of bark colour, as certain colours appear to be characteristic of particular sections of the genus, (e.g. chestnut-brown in the *Leiocarpae* and red-purple in some *Maculatae* and *Stellatae*).

3.4.1.2 *Stem texture*

Canes of the *Leiocarpae* are more lustrous than those of other taxa, suggesting that the composition of waxes on these canes differs from that of other *Actinidia*.

The texture of the canes results from the quantity and quality of the indument (hair-covering) and any underlying processes of bark formation. The

indument or hair-covering is recognised as the most important taxonomic character (Dunn 1911, Li 1952, Liang 1984). Descriptions of cane hairs agree with those of previous authors, except that *A. rufa* have pubescent canes unlike those of other *Leiocarpae*. Other authors seem unaware of this fact and the taxonomy of this plant may need to be re-examined.

Taxonomists have documented obvious properties of hairs such as presence/absence and texture, but there is a greater need for precise descriptions of the extent and degree of hair persistence. Cultivars of *A. deliciosa* and genotypes of *A. chinensis* can be recognised by the form of the hairs at maturity, whether they consist of entire hairs, partial stubble or the hair bases only. To describe the stems of *A. chinensis* for instance as "smooth" is an oversimplification, it is more a matter of degree, i.e. the length and form of the hairs at maturity. Stereomicroscopy can be used to count the density of hair bases on an apparently smooth stem.

Lenticels are poorly or incompletely described by most taxonomists working with *Actinidia*. Krüssmann (1984) has recognised the value of lenticel colour, but I suspect that his observations are derived from summer shoots, which are more brightly coloured than winter shoots. The character "lenticel density" appears to distinguish taxa to the sectional level, and even within sections and species, distinctive plants emerge such as *A. rufa* and *A. deliciosa* cv. Bruno, on the basis of lenticel characters. Lenticel colour and shape were used in descriptions of *Actinidia* by Vorobiev (1939) and Anon. (1979). The best descriptions of lenticels are those of Zhang and Thorpe (1986), which include details of the size, colour, relative distribution and density of lenticels, also lenticel protuberance is documented for 12 cultivars of *A. deliciosa*.

3.4.1.3 *Bud shape*

Bud shape changes with development of the cane (Hildebrand 1883). Initially, in *A. deliciosa* for instance, buds are spherical and evenly proportioned and the ostioles are poorly developed. With subsequent growth the bud-case becomes taller and increasingly rectangular in form. For taxonomic studies, buds should be selected from mid to basal regions of the cane, where bud shape has ceased to change i.e. buds are fully "mature".

The shape of the bud-case is at its most uniform in winter and the buds appear as described in this chapter. During bud-burst the ostiole ruptures and the bud-case becomes swollen in the middle, and creased and contracted at its base. Bud morphology should not be used for identification at this stage. Examination of the buds in mid-summer reveals a number of shallow to elongated buds, with

ostioles delimiting the remains of withered or inactive buds. These are aborted buds which failed to burst in the current season and should not be used in taxonomic work.

Many of the morphological characters employed in this study could be readily adapted for studies of bud development, or they might be used at pruning time, as correlative indicators of the likelihood of a shoot to flower. Within a taxon some buds, appear plumper than other winter buds and these are often associated with thicker (larger diameter) canes. Cane diameter might be used in this way. This character gives a relatively poor separation of *Actinidia* taxa other than *Leiocarpae* (Figure 3.4.10). Shoot morphological characters could be exploited to improve the accuracy of winter pruning, as similar work has been done for sultana vines in Australia (Antcliff, Webster and May 1958). These authors found that the most fruitful canes had :

> Well-ripened appearance, good diameter throughout, internodes not too long, and the presence of persistent laterals.
>
> Antcliff *et al.* (1958), page 328.

Many of these characters were also used to assess the productive characteristics of fruiting arms in 9 pistillate clones of *A. deliciosa* (Zhang and Thorp 1986, Table 5, page 162).

Bud shape is best characterised by the ratio of bud length to bud height (Figure 3.4.6), or by describing the shape and symmetry. This information could be readily incorporated into taxonomic descriptions of *Actinidia*. Infraspecific variation may be considerable, but the basic form of the bud is "intuitively" recognisable for a given taxon.

Bud form is such a reliable taxonomic character that even its individual components can be used to discriminate between varieties and forms at the lowest levels of classification (Zhang and Thorp 1986 and the present study).

While I am in general agreement with the findings of Zhang and Thorp *loc.cit*, some of their terminology is vague, for example, buds of *A. deliciosa* cv. Gracie are described as :

> indistinct, with a convex distal face
>
> page 590.

It would be more precise to describe the relative length of the distal bud face and to distinguish between the shape of the distal face above and below the ostiole, as I have done. Some of the diagrams of winter buds provided in Zhang and Thorp *loc.cit* (Figure 1, page 590) are exaggerated and would need to be supplemented with verbal descriptions for use in routine taxonomy. Bud emergence characters are

discussed in Section 4.3.4 in relation to temperature, as these are influenced by geographic factors to a considerable degree.

3.4.2 Cluster analysis of winter shoot characters

Cluster analysis (C.A.) is used to explore the taxonomic potential of the morphological characters, derived from winter deciduous shoots of 32 *Actinidia* taxa.

C.A. is objective and consistent in its mathematical execution, but subjectivity arises in the selection of variables (characters) and in the interpretation of the resultant groupings or "clusters" (Sneath and Sokal 1973). It must be noted that C.A. is only as representative of the data set from which it was derived.

Comparison of independent clustering or "linkage" methods permits an assessment of "real" taxonomic groupings. Natural groups are indicated by those assemblages which arise repeatedly and independently of the different linkage methods, e.g. clusters "A" and "E" in this study.

The combination of subclusters "1" and "3" corresponds to members of the *Leiocarpae* (Liang 1984). Subcluster "3" represents members of series *Lamellatae*, characterised by plants with a chambered pith and subcluster "1" is recognised as series *Solidae*, defined by the presence of a solid pith (Liang 1984).

Clusters "A" and "B" represent varied assemblages of *Maculatae* (Dunn 1911) and *Strigosae* (Li 1952) studied. These sections are defined as those plants with spotted fruit and strigose hairs respectively. The groupings within these clusters are at variance with the current subdivision of the genus which asserts that *Maculatae* and *Strigosae* are separate groups, i.e. they ought to cluster separately.

Cluster "B" comprising the genotypes of *A.indochinensis* is removed from other *Maculatae* to which it is allegedly related. Evidence from winter shoot morphology might suggest that a re-examination of *Maculatae* and *Strigosae*, as they now stand, may be warranted.

Clusters "C" and "D" together include the exemplars of Section *Stellatae* (Li 1952) those *Actinidia* with stellate foliar hairs. This grouping segregates early from other *Actinidia* and contains the infraspecific taxa of *A. deliciosa* as cluster "C". Subclusters "4" and "5" form consistent cultivar groupings, such as the "Abbott-Allison" and "Gracie-Jones" alliances as recognised by Zhang and Thorp 1986, although a greater number of cultivars were observed in my study. The cultivar 'Jones' is now regarded as a grafted form of 'Gracie' (Jones pers. comm, in Zhang and Thorp 1986).

Mouat (1958) and Astridge (1975) had earlier separated some of these cultivars on the basis of morphological characters such as: fruit size and shape, number of flowers per inflorescence, and form and orientation of floral parts such as petals and stigmas.

Groupings of *A. deliciosa* cultivars derived from winter shoot characters (subclusters "4" - "6") do not agree with those predicted from comparisons of fruit shape (Figure 3, Zhang and Thorp 1986). Subcluster "4" includes cultivars with shorter buds, subcluster "5" contains those with long buds. Cultivars 'Hayward' and 'Elmwood' group together because their buds are of average length, but they have larger ostioles with externally protuberant winter shoots.

Cluster "B" is a variable assemblage of lower altitude *Stellatae* which were originally obtained from lower altitudes and this includes plants with exposed buds. Undoubtedly, the *Stellatae* would cluster more naturally with a better representation of taxa, than the present study allows, since the C.A. is biased in favour of *A. deliciosa*. Caution is certainly advised in the use of vegetative characters in descriptions of *A. chinensis*, as this is an extremely variable species and like *A. deliciosa*, infraspecific variation can be considerable.

Data on winter shoot morphology suggest that *A. callosa* var. *henryi* is extremely variable, compared to other *Maculatae* studied. Its position in Figures 3.5 and 3.6 arises from the fact that it is the only taxon in this study with more than one shoot per bud (see Table 3.11, Appendix 3.1).

Clustering by average-linkage (Figure 3.5) produces less stringent groupings and as a result *A. callosa* var. *henryi* associates, albeit remotely, with the *Maculatae*, *Strigosae* alliance. *A. callosa* is distinguished from other *Actinidia* in this study, in that it occurs further west than other species and it is the only taxon known to have contact with the Himalayan flora (Liang 1983). *A.rufa* clusters with the *Maculatae-Strigosae* alliance and on the basis of its tomentose stems, its current classification in the *Leiocarpae* may be questionable.

The quality of the cluster analysis may be seen by the fact that the clusters produced are generally explicible; further the phenograms are representative of the similarity matrix (Appendix 3.2), as the cophenetic correlations (Tables 3.7 to 3.10) mostly range from 0.72 - 0.74 (1.00 is maximum).

The application of discriminant procedures confirms the validity of groupings generated by cluster analysis. More intensive statistical analysis of the characters has shown the importance of ostiole size and bud-height in separating (discriminating between) the groups under study. Although the most useful characters have the highest discriminant efficacy, this does not preclude the use of lesser discriminating characters (such as cane colour or hair density), as aids to

identifying specific taxa, (e.g. *A. eriantha*, white woolly canes); the mostly chestnut brown canes of *A. arguta* types.

3.4.3 Bud form in relation to temperature and geography

Winter minimum temperature is one of the more important factors governing the distribution of horticultural crops in the world (Westwood 1988, Krussmann 1984). It is the one factor which is the least amenable to manipulation by the orchardist or field-based researcher.

Actinidia is one of the few genera which tolerates a range of winter temperatures from those of Siberia to Indonesia. As *Actinidia* are mostly winter-deciduous vines, the temperature tolerance of these plants must be linked to the structural and physiological protection afforded by the winter shoots. Flower buds of *A. deliciosa* can tolerate temperatures as low as -2°C, but winter dormant shoots tolerate temperatures as low as -10°C (Hewett and Young 1981). *A. kolomikta*, the only species with a "distribution centre" in the U.S.S.R., is known to tolerate temperatures as low as -45°C (Michurin 1949). *Actinidia arguta* is another member of the *Leiocarpae* with concealed buds, which extends as far north as Japan and the U.S.S.R. In addition, *A. arguta* is reported to grow well and fruit in cool-temperate regions of the world such as Kew in the U.K. (Bean 1972) and Washington D.C., U.S.A., (Fairchild 1927, Rehder 1951).

Bean (1972) also describes a thriving specimen of *A. kolomikta* at the R.H.S.[2]Garden at Wisely, U.K. This account should be contrasted with the meagre stature and performance of the *A. kolomikta* plant growing in the warm temperate site near Auckland, N.Z.

The winter buds of *Leiocarpae* such as *A. arguta*, *A. kolomikta* and *A. polygama* have been described by Feist (1887), Hildebrand (1883), Lubbock (1899); Poyarkova (1949) and Ferguson (1990a) These taxa can be widely separated in the wild, but all predominate at higher altitudes and extend furtherest into the colder regions of N.E. Asia (e.g. Japan, U.S.S.R.), than other *Actinidia* (Liang 1983). These taxa have small, shallow buds with bud parts (shoots) sunken deeply into the protective tissues of the stem cortex and the petiole base. Ostioles of these buds are diminutive except for *A. arguta* var. *cordifolia.* Conversely, buds of *A. chinensis* are taller in profile with large ostioles delimiting many visible bud structures. Exposed bud structures (shoot and protective structures)

[2]R.H.S. = Royal Horticultural Society.

components predominate at lower latitudes and altitudes (see Gui 1981, Ferguson 1990b). Blanchet described the effects of devastating winter frosts on *Actinidia* growing in an experimental garden (variety collection) in S.W. France :

> ...during the exceptional frosts in the winters of 1985 (-25°C) and 1987 (-20°C). Of the accurately determined species the only ones to survive were *arguta, kolomikta, polygama* and *melanandra*. On the same plot, the *Actinidia chinensis* plants which were the same age, were destroyed and had to be cut back to the base.
>
> Blanchet (1989), page 543.

The maps of *Actinidia* distribution contained in Liang (1983) show that the northernmost limits of Section *Stellatae*, and most other *Actinidia* (Dunn 1911), coincide with the number of frost-free days and the mean January isotherms (Tregear 1980). The northern and southern limits of the *Stellatae* correspond to the ranges of the evergreen broad-leaf forest zone in subtropical China, and the mixed deciduous and broad-leaf forest zone in the northern subtropical zone (Liang 1975). This indicates a significant change in regional climate.

Although the broad regional picture of *Actinidia* distribution is well documented by Dunn (1911) and Liang (1983), the local patterns of distribution are undoubtedly more complex. Climatic conditions at a given point in China result from the interaction of latitudinal (proximity to the tropics) and altitudinal gradients. Altitudinal data alone may be misleading, as *A. kolomikta* extends from 800-1500 m and is the most cold-tolerant of all *Actinidia*, whereas, further south *A. chinensis* var. *hispida* (syn. *A. deliciosa*) ranges in altitude from 800-1400 m (Liang 1984), and is relatively frost-sensitive. China is generally mountainous further inland with lowland regions along the river courses (Tregear 1980). The average altitude increases in a westerly direction from Taiwan to Tibet. Members of the genus as a whole may occupy altitudes ranging from 100-2700 m (Liang 1984), but some geographically heterogeneous provinces, (such as Guangxi in the south west and Henan in the north), contain nearly all 50 or so species of the genus (Gao 1988, Liang 1983).

Climatic factors are not the sole determinants of plant distribution ; proximity to the biogeographic centres of floristic diversity is also important. For instance, Taiwan has a climate perfectly suited to the growth of many *Actinidia*, but only 5 taxa are present (Liang 1983, Table 1).

Examination of the 18 genotypes of *A. chinensis* var. *chinensis*, which were originally obtained from inland and coastal provinces at different altitudes and latitudes, suggests that bud morphology is responsive to temperature. Genotypes obtained from higher altitudes in Hunan and Lushan Mtn in Jiangxi, show

"*Leiocarpae* trends", but on a much smaller scale. The form of these buds is still recognisable as that of *A. chinensis* var. *chinensis*, but dimensions of variables such as bud-height, ostiole size and petiole scar diameter (L.P.D.), are much smaller in these plants from colder regions of China.

Some of the clines (gradients of continuous morphological expression) seen in hair density and softness from coastal to inland forms of *A. chinensis* (Liang 1975, 1982a), are also evident in material grown in the *Actinidia* germplasm collection. This indicates that these clines are genotypically based. These genotypes may form ecologically separated races (ecotypes) in China and they may in time become further differentiated morphologically and reproductively to form species. From the distribution of these taxa in the wild (Liang 1975, 1982a, 1983) and the general morphology of the buds, it can be inferred that most of the *chinensis* genotypes studied are *A. chinensis* var. *chinensis* - the soft-haired mihoutao.

From Chapter One it was noted that *A. chinensis* was formerly regarded (Liang 1975) as a polymorphic species composed of three geographically distinctive varieties, namely : soft-haired (var. *chinensis*), stiff-haired (var. *hispida*) and the spiny-haired (var. *setosa*) forms. The soft-haired form is characteristic of coastal and eastern China (Liang 1975, 1982a).

The stiff-haired form mainly occurs in westerly or inland (colder) regions of China. Both varieties overlap in Southern Shensi and mountainous regions in the west of Hupei and Hunan whereas var. *setosa* is confined to Taiwan. Liang and Ferguson (1984, 1986) renamed these taxa as :

A. chinensis var. *chinensis* (Soft-haired)

A. chinensis var. *deliciosa* (stiff-haired)

and *A. setosa* (spiny-haired form).

Separation of soft and stiff-haired varieties of mihoutao is not always easy, particularly in regions where the distributions of both types overlap. In some provinces, (e.g. Hubei), the plants cannot be distinguished on the basis of leaf form alone (Liang 1982a, Ferguson 1990b), which is usually diagnostic of these taxa viz : abrupt apices of var. *deliciosa* and retuse ones in var. *chinensis*.

The situation is further complicated by the existence of transitional forms between soft and stiff-haired varieties, e.g. *A. chinensis* var. *jinggangshanensis* (Liang and Ferguson 1986). Such transitional forms may provide evidence of natural hybridisation between these taxa (Liang 1982a, Ferguson 1990b). Some genotypes of *A. chinensis* var. *chinensis* in the germplasm collection, such as G4B3 (Guangxi) and G4D2 (Jiangxi), have unusually elongated buds; this which may indicate possible evidence of hybridisation with *A. deliciosa* in the past. The

existence of such morphological intermediates between these taxa suggest that speciation is a relatively recent phenomenon. *A. deliciosa* being the hexaploid is most likely derived from *A. chinensis*, which is normally a diploid (McNeilage and Considine 1989).

Intrataxal variation can be considerable in widely distributed taxa such a *A. chinensis* and *A. arguta* and this is reflected in the nomenclatural history of these plants. *A. arguta* for instance, has been treated as a polymorphic species composed of several varieties (Dunn 1911, Li 1952, Liang 1984), or as a several different species (Bean 1972, Rehder 1951, Vorobiev 1939). The current taxonomic groupings of Liang (1984) appear to be mostly supported by cluster analysis of winter shoot characters (Figures 3.5, 3.6). According to Li (1952), *Actinidia purpurea* represents the counterpart of *A. arguta* in southwestern China and might possibly be treated as a variety of *A. arguta.*

He says of *A. arguta :*

> The several varieties here recognised occur in more or less contiguous areas and pass into each other imperceptibly by intergrading forms. Clearly this is another of the very widespread, more or less polymorphic species characteristic of the genus *Actinidia.*
>
> Li (1952), page 31.

The relationship between bud structure and temperature is supported by variation within genotypes of buds in the one taxon (*A. chinensis)* in geographically varied environments. There is a general convergence of bud morphology between members of different sections of the genus, obtained from similar environmental conditions in the wild. Buds of higher altitude *Stellatae* such as *A. deliciosa* and some genotypes of *A. chinensis* show similar trends in bud-height and ostiole size to *Leiocarpae* growing at similar altitudes. These plants are from opposite ends of the spectrum in terms of their chromosome numbers (McNeilage and Considine 1989), morphological advancement (Liang 1983) and taxonomic treatments (Dunn 1911, Li 1952, Liang 1984).

The degree of internal bud protection in *Actinidia* is inversely related to the degree of external protection. Tall buds with large ostioles such as *A. chinensis* are susceptible to freezing damage and this necessitates a large investment by the plant into internal protective structures, such as : increasingly lignified scales and transitional leaves, and an abundance of insulating hairs. This occurs to a limited extent in some of the more cold-tolerant ecotypes of *A. chinensis* var. *chinensis.* These lignified structures appear to have a lower water content and would be less susceptible to freezing damage. The most cold-tolerant

Actinidia, (such as *A. kolomikta*), have relatively few modified leaf structures (if any). The leaves are soft, membranous and fleshy and outer leaves are represented by transitional leaves with minimal lignification, if any at all. However, the tips of these transitional leaves have phenolic pigmentation. There would be no benefit to the plant in diverting assimilates into scales or similar protective structures, if the buds are deeply buried in cortical tissues, i.e. the protection afforded by the stem is adequate in itself. The most cold-tolerant *Actinidia* rely on the stem as a means of protecting winter shoots, whereas, more temperate plants place greater reliance on leaf structures as a means of thermal protection.

Morphological observations reveal only part of the temperature tolerance story, namely, the capability for frost-tolerance by thermal insulation. Literature reviewed by Wieser (1970) and Sakai and Larcher (1987) shows that plants can tolerate freezing by either chemical or physical removal of water (dehydration), or by depressing the freezing point by increased concentrations of osmotica, (e.g. sucrose). Plants may even promote extracellular freezing by secretion of ice-nucleating substances, (e.g., H_2O), in regions such as : the apoplast (free space continuum between microfibrils in cell walls), the mesophyll air-spaces, or the eternal (abaxial) surfaces of buds. Recent evidence (Guy 1990) shows that seasonal acclimation to low temperatures is correlated with isozymic shifts in key enzymes and quantitative and conformational alterations of selected gene products. It may be possible to alter the temperature tolerance of existing cultivars such as 'Hayward' by the application of genetic engineering technology. Future research on physiological and molecular changes associated with freezing of *Actinidia* buds is warranted.

3.4.4 Emergence from bud dormancy

Moderately low temperatures $\geqslant 10^{\circ}C$ can be beneficial in increasing the efficiacy of bud-break in *Actinidia.*

Entry of buds into winter dormancy requires an accumulation of short-days (S.D.) which is mediated by the phytochrome system (Vince-Prue 1985). Maintenance of this dormancy in buds of *A. deliciosa* cv. Bruno involves the accumulation of ABA-like inhibitors, which are stored in the tissues of the bud-cover. This structure also imposes dormancy by acting as a mechanical barrier to penetration of light and oxygen (Lionakis and Schwabe 1984a).

"Dormancy-breaking" (Vegis 1964) necessitates an accumulation of hours below a threshold temperature, (e.g. $10^{\circ}C$), termed the chilling requirement, which is thought by some to be 800 Richardson chilling units (Ferguson 1990a). As the

N.Z. climate is characterised by warm winters (Jackson 1986, Wratt and Smith 1983), the chilling requirement of deciduous fruit crops, such as apple and kiwifruit, is often only marginally or incompletely satisfied. Inadequate winter chilling lowers the productivity of these crops by reducing the incidence of bud burst and the numbers of flower buds formed. In addition, the duration of flowering and harvest peaks are spread over a much longer period (Ferguson and Davison 1986).

There may be considerable differences in the time from bud-break to harvest when the same cultivar is grown in different regions. 'Hayward' vines grown in Invercargill undergo bud-burst prior to those in Auckland, because the chilling requirement is satisfied in southern regions of N.Z. Although buds on vines further north are the last to burst, the favourable climatic conditions for growth (presumably higher temperature and humidity) increase the growth rates of these vines, so that eventually fruit from vines in Auckland is harvested before that in Invercargill. Growers in the Nelson region release their crop 10 days ahead of North Island orchardists, because Nelson has the ideal balance between adequate chilling-hours and the warm temperatures required for rapid growth (M. Morley-Bunker pers. comm.).

The chilling requirements of different *Actinidia* need to be studied to produce cultivars with lower chilling requirements in the future. More exposed buds such as *A. chinensis* ought to be correlated with lower chilling-requirements, but this hypothesis requirement of *A. deliciosa* cv. Abbott is not reflected in a distinctive bud morphology, as far as the present study indicates.

Determination of budbreak may be more complex than fulfilment of chilling requirements alone. Recent studies demonstrate the importance of temperatures at the time of bud-burst in *A. deliciosa* cv. Hayward, to quote :

> ...each 1^{o}C rise in temperature over the budbreak period, reduces the spread of budbreak by three days and increases the proportion of overwintering buds that break by 4.5%...
>
> Stanley *et al.*(1988), pages 12-14.

3.4.5 Bud morphology and breeding potential of *Actinidia*

The diversity of bud characters seen in winter shoots of *Actinidia*, suggests that kiwifruit cultivars of the future could have markedly different properties than those of 'Hayward'.

3.4.5.1 *Cold tolerance*

The cold-tolerant *A. kolomikta* buds of U.S.S.R. with their minute ostioles and deeply concealed shoots have long been used to breed cold-tolerant *Actinidia*. The Soviet horticulturist Michurin said of his selections :

> They originate from Kabany Klyuch, a locality in the East Siberian taiga. In this area *Actinidia* has for many decades withstood frosts of as much as 40 to 45°C below zero, which in some years set in before the ground was covered with snow.
>
> Michurin (1949), page 433.

Michurin produced 5 new cold-tolerant varieties of *Actinidia*, three of these were based on *A. arguta* and two on *A. kolomikta*. Ferguson (1990a) suggested that *A. kolomikta* might be used in the production of cold-tolerant root-stocks, to decrease the sensitivity of vine stems to frost damage. [From Chapter Two, it is apparent that *kolomikta* root-stocks might reduce the vigour of the vines under N.Z. conditions, which could be an added bonus.] Mature vines are apparently more frost-tolerant than juvenile plants, although further data are needed to define these responses.

3.4.5.2 *Bud-break and flowering time*

The timing of bud-break and hence flower development seems to be correlated with the susceptibility of *Actinidia* to late spring frosts. In general, indigenous *Actinidia* growing further south have earlier bud-break and fruit maturity than more northerly populations (see Liang 1984). The most temperature-sensitive Chinese species *A. indochinensis* and *A. chinensis* var. *chinensis* undergo anthesis in March and April, respectively, whereas other *Actinidia* sp. enter anthesis in May or June. Even the most temperature-tolerant species *A. kolomikta* exhibits marked phenological differences according to habitat. Plants of Sichuan province in S.W. China undergo anthesis in late May, whereas those of N.E. provinces do not reach anthesis until early in July.

Phenological differences appear to be genotypically based. Blanchet (1989) reports similar flowering times among *Leiocarpae* and *A. chinensis*, growing in a horticultural variety collection in S.W. France.

Current kiwifruit production is based mainly upon *A. deliciosa*. This is a perennial, deciduous vine growing in high mountain forests, from 800-1400 m in altitude (Liang 1984). As a result, present cultivars such as *A. deliciosa* cv. Hayward show late flowering and fruiting behaviour (U.P.O.V. 1981) and they frequently have higher dormancy-breaking requirements than are realised by warmer regions of temperate climates such as those of N.Z. Plant-breeders should

be aware of the potential afforded by widely distributed, polymorphic taxa such as *A. chinensis*. Ecotypes of *A. chinensis* var. *chinensis* from Lushan mountain might be used to produce cultivars in temperate or cool-temperate climates, whereas those from coastal Guangxi could be used for selections in warm-temperate areas. Thus, two cultivars based on these extreme ecotypes might have the enhanced flavour of *A. chinensis*, in conjunction with very different dormancy-breaking ("chilling"), temperature tolerance and phenological properties (early vs. late maturing cultivars).

The development of earlier maturing *Actinidia* cultivars would improve the chance of pollination, which is currently limited by asynchronous flowering behaviour between male and female cultivars (Brundell 1975c). This might decrease the need for artificial pollination (Hopping 1985). It would therefore be logical to develop new female cultivars based on genotypes from more southerly (earlier flowering) regions of China. The development of early maturing cultivars, could reduce the need for long-term post-harvest storage facilities by marketing of early and late cultivars, as currently exists in the apple industry (Jackson 1986).

Vines from more tropical regions, such as *A. indochinensis* and *A. latifolia* (Dunn 1911, Liang 1983), have buds which break to produce new shoots on the current year's wood (Ferguson 1990a), in contrast to most other *Actinidia* (Dunn 1911, and this chapter). Such taxa could be used to develop new kiwifruit cultivars with lower chilling requirements in temperate areas, and hence increased bud-break.

Dormancy-breaking problems could be lowered or eliminated altogether by developing *Actinidia* selections based on semi-evergreen taxa, such as *A. melliana* or fully-evergreen plants (e.g. *A. fulvicoma* and *A. liangguangensis*). This would require the development of an entirely new production system associated with year-round cropping practices, as currently exist in the citrus industry (Jackson 1986). However, increased production costs associated with pruning and irrigation might offset any advantages associated with cropping evergreen *Actinidia*.

3.4.5.3 *Bud productivity*

Poor or uneven budbreak currently limits the productivity of existing kiwifruit cultivars such as 'Hayward'. For instance, bud-burst may be as low as 30-50% in *A. deliciosa* cv. Hayward (Stanley *et al.* 1988). Data from Brundell (1975c) and Zhang and Thorp (1986) show that 'Hayward' is the least productive in terms of bud-break, among the *A. deliciosa* cultivars. Cultivars such as 'Monty' might be used as a basis for developing more productive selections.

Bud productivity of *Actinidia* might be increased in commercial cultivars by artificial hybridisation using other species of the genus (Ferguson 1990d).

1. The number of buds per m^2 of canes could be increased by shortening of the internodes. This could be affected by hybridisation with *Leiocarpae.*
2. The number of productive floral units per bud could be increased by hybridisation with some *Leiocarpae*, which can average 1-7 flowers per inflorescence. *A. latifolia* of the *Stellatae* may have up to 20 flowers per cyme and this could also be used in breeding.
3. The number of shoots per bud could be increased by hybridisation with plants such as *A. callosa* var. *henryi* of the *Maculatae.*
4. The percentage bud-break might be increased in cultivars of the future, by greater use of ecotypes of species such as *A. chinensis.* Cultivars based on lowland ecotypes could be used to decrease the chilling requirements of vines for cultivation in warm-temperate areas. Cultivars based on mountain forms, such as *A. deliciosa*, could be grown in more temperate climates.

It should be noted that increasing the number of productive units on the shoot, will not eliminate problems arising from heterogeneity associated with the pruning and training system of the vine (see Chapter Two). The distance of buds from the bases of horizontal canes determines, in part, whether or not buds will be floral or vegetative (Brundell 1975c).

Benefits that might accrue from increased yields would need to be weighed against any additional production costs. Increasing the number of flowers per inflorescence would increase the number of fruit per hectare. Disadvantages of improving fruit yield might include greater financial costs associated with "fruit-thinning" (selective removal of fruit to improve average fruit weight, usually in relation to pre-set yield targets per vine). The incidence of cosmetic "fruit-grading" defects such as "windrub" might increase with greater numbers of fruit per inflorescence. Such fruit are currently rejected for export and result in a loss of revenue to the grower.

It is likely that as more countries develop kiwifruit industries, emphasis may shift from ways of increasing yield to ways of improving fruit quality and the diversity of cultivar attributes. The N.Z. kiwifruit industry is rapidly facing such challenges. Concern about fruit quality has led to a big debate in the N.Z. industry, as to whether or not a producer board is needed to regulate the price and quality of kiwifruit bound for overseas markets.

3.5 CONCLUSIONS

1. Most of the variation described in winter shoots of *Actinidia* from the kiwifruit germplasm collection is genotypic in nature.
2. Winter shoot characters associated with cane surfaces, bud shape and bud emergence can be used in identification of *Actinidia* as verified by multivariate analysis. Discriminant analysis indicates that bud-height and ostiole size characters optimise the separation of the major groups under study. The use of ratio variables may need to be reconsidered in future multivariate treatments of these characters.
3. Bud-protection characters such as ostiole size may traverse taxonomic groupings, as the former have evolved in response to geographic factors such as temperature.
4. Plants of the *Leiocarpae* and *Stellatae* emerge as natural assemblages in cluster analysis.
5. The current classifications of *A. rufa* and *A. callosa* var. *henryi* (Liang 1984) is in doubt.
6. Infraspecific variation can be considerable in widely distributed polymorphic taxa such as *A. arguta* and *A. chinensis*.
7. Winter shoot characters displayed by other species of the genus *Actinidia*, e.g. particularly those of the *Leiocarpae*, may offer the potential to genetically increase : cold-tolerance, advance the time of flowering and to increase floral productivity of existing cultivars, (such as 'Hayward').

CHAPTER FOUR

GENERAL DISCUSSION

CHAPTER FOUR

FINAL DISCUSSION

4.1 CONTEXT OF PROBLEM

This thesis evolved as an exploratory study of the taxonomic potential of vegetative morphological characters in *Actinidia* taxa, based on plants grown in the D.S.I.R. germplasm collection. This study also includes synthesis of information from the literature, together with examination of herbarium specimens from Asia. Plants in this collection are cultivated for their possible relevance to horticulture and plant breeding. It has not been practical to examine all taxa of *Actinidia*, due to the difficulty of obtaining specimens from China.

Vegetative characters are emphasised. Previously *Actinidia* taxonomy has been based on morphological characters of the summer shoot, but much of this information is incomplete. In this thesis, therefore, emphasis has been directed towards completing this information. At the same time, I have examined the potential for use of winter shoot characters in *Actinidia* taxonomy. Previous workers have largely ignored features of the winter shoot. Plants were mainly selected from Sections *Leiocarpae* and *Stellatae* because, collectively, they include the most widely distributed and morphologically diverse taxa of the genus.

4.2 CLUSTER ANALYSIS OF THE COMBINED DATA SET

The use of cluster analysis permits us to assess the ability of the characters chosen to generate taxonomic structure. This emerges as a test of the integrity of possible groups arising from the data set. The data generate robust and repeatable clusters whose composition agrees with that of Sections *Leiocarpae* and *Stellatae*, as predicted by the classification of Liang (1984). This is the first application of numerical taxonomy to members of this morphologically diverse and complex genus and results to date are mostly encouraging.

The best attainable groups in this study are those generated from a combined set of 80 characters derived from winter and summer shoots. Examination of the correlation matrix of all characters shows that both sets of characters are statistically independent of one another (few correlations, Appendix 4.2), so that conclusions in this thesis are based on two independent lines of morphological evidence.

The combined phenogram (Figure 4.1) derived from clustering by average-linkage generates three clusters at an acceptable similarity level of 0.61.

Table 4.1 Linkage Coefficients (average)

OTU		Linkage coefficient
15	Chin3/6/14b	0.9336
16	Chin460.4	0.9248
17	Chin460.9	0.8237
18	AdelBruno	0.9017
19	AdelHay	0.8939
20	AdelMatua	0.8455
21	AdelChlorocarpa	0.6842
13	Latif	0.7671
14	Erian	0.4834
1	Argarg	0.7610
2	Argcord	0.6963
6	Polyg3/12/11	0.8601
7	Valv	0.7407
5	Kolom	0.6379
12	Hemsley	0.6017
9	Chrys	0.8311
10	Indoch36/3/11a	0.6618
8	Callhen	0.6445
3	Rufa	0.6166
11	Mell	0.4122
4	Melan	0.0000

Cophenetic correlation = 0.937

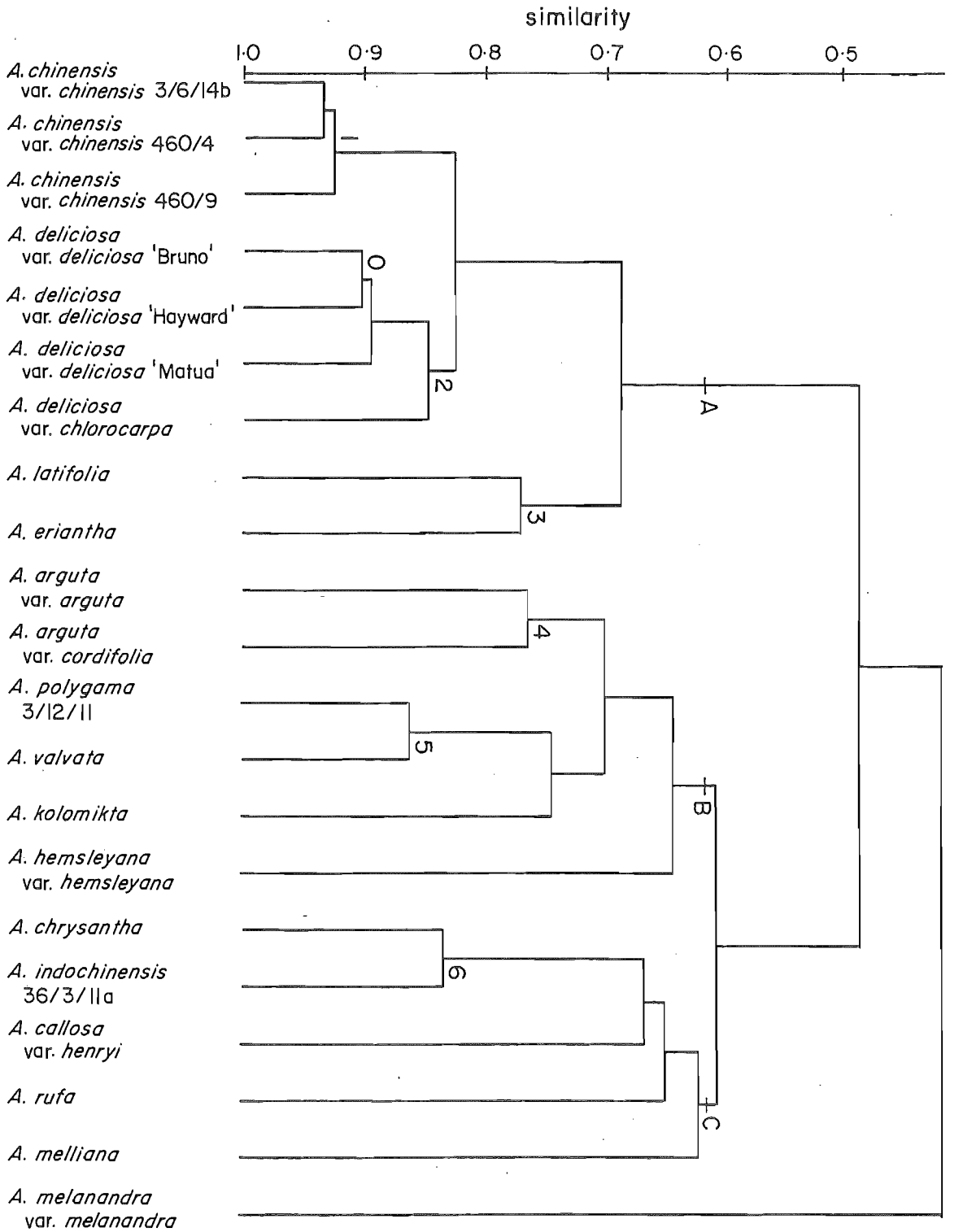


Figure 4·1: Cluster analysis of combined data set using average-linkage

Cluster "A" comprises members of Section *Stellatae* Li, collectively the infraspecific taxa of the diploid species *A. chinensis* and the hexaploid species *A. deliciosa*, in this study. These are known to be closely related in the wild, with intergrading morphologies where the distributions of these taxa overlap (Liang 1975, 1982a,b).

Cluster "B" includes members of Section *Leiocarpae* which are subdivided in a different place to the "solid-pith", "lamellate-pith" boundary recognised by Liang (1984) in his recognition of Series *Solidae* and Series *Lamellatae*, respectively. Here, cluster analysis has weighted the classification in favour of the character "variegated" or "non-variegated" leaves. Such a discontinuity is supported by important reproductive characters such as maximum number of flowers per cyme and anther colour, whether "melanic" or "orange-yellow". The former is an important character state as it is uniquely derived in the *Leiocarpae* - together with, the character "non-lenticellate" (unspotted) fruit. Chemotaxonomic studies of carotenoids and/or phenolics might elucidate where Section *Leiocarpae* should be split, in accordance with Liang's subdivision, or that suggested by flower number. Gilg (1893) originally subdivided the entire genus into uniflorous or multiflorous types prior to the taxonomic revisions of the genus by Dunn (1911) and Li (1952).

Cluster "C" shows poor taxonomic structure with much chaining at low levels of similarity. Members of this cluster associate because they are less dissimilar to one another than to everything else. The taxonomic structure of Sections *Strigosae* and *Maculatae* can only be explored properly with a much greater representation of taxa. Important constituents of this cluster include *A. rufa*, currently placed in the *Leiocarpae* (Liang 1984) and the close-knit pair of allopatric species *A. indochinensis* and *A. chrysantha*. Morphological characters of *A. rufa* which are at variance with other *Leiocarpae* include densely hairy stems and branched trichomes on the lower surface of the leaf. Redgewell (1983) argues for removal of *A. rufa* from the *Leiocarpae* on the basis of its mucilage composition, but his suggestion to transfer this taxon to the *Stellatae* may be somewhat premature on the basis of current morphological evidence.

A. melanandra, with a linkage coefficient of zero (Table 4.1), is the major "outlier" of the tree (Figure 4.1). Examination of the Gower similarity coefficients (Appendix 4.2), however, shows that *A. melanandra* is most similar to *A. argata* var. *cordifolia*. The distinctive combination of small, and coriaceous leaves in *A. melanandra* may explain its anomalous placement in Figure 4.1.

The taxonomic revisions of Li (1952) and Liang (1984) suggest that abaxial foliar trichomes are simple (unbranched) in all but the *Stellatae*, but microscopic observations of these plants do not substantiate this view. Examination of some *Maculatae* (including Chinese herbarium specimens determined by C.F. Liang, Appendix 2.3.1), has shown that abaxial foliar hairs are often complex in structure, with some taxa (e.g. *A. cylindrica* var. *reticulata*) showing transitions toward the "non-stalked, stellate" hair type of Section *Stellatae*. This raises profound questions concerning the taxonomic validity of Sections *Maculatae* and *Strigosae* and/or the marker characters currently delimiting these groups. Inspection of the diagnosis in the *Flora Reipublicaris Sinicae* (Liang 1984) suggest that *Maculatae* and *Strigosae* are heterogeneous alliances of species; many of the characters delimiting these groups are common to other sections of the genus. The *Maculatae* reiterate the solid and lamellate pith types of Section *Leiocarpae*, but differ from the former in their lenticellate fruit. This is not a good marker character, since it is common to three out of four sections of the genus. The variation expressed between sections of the genus may well be continuous, but this does not excuse taxonomic inaccuracies within classification of this genus. Dunn (1911) noted that the *Maculatae* were geographically and morphologically intermediary between *Leiocarpae* and *Vestitae*[1]. A re-examination of subgeneric classification of *Actinidia* is clearly warranted, using as many taxa as possible.

It is easy to become pre-occupied with the business of forming groups, but it should be remembered that characters are the only (concrete) units of taxonomic reality, which exist independently of the groups that they form. Groups may be demonstrable through statistical means (correlation matrices, phenetic and cladistic trees), but essentially they exist in the minds of taxonomists. Taxonomy then, is the art of abstracting groups from the science of collating characters. There may however be much art in the coding and formulation of characters, since the taxonomist is frequently required to express continuous variation in terms of discrete taxonomic units, termed character states. Definition of characters will always be the major obstacle in achieving any objective classification.

[1]Dunn's *Vestitae* were an amalgam of *Strigosae* and *Stellatae* as defined by Liang (1984).

4.3 DEFINING TAXONOMIC GROUPS

Taxonomic groups at all levels have a "basic identity" which is expressed over a finite "range" of variation.

4.3.1 **Taxonomic "identity"**

The identity of a taxonomic group may be thought of as "the combination of correlated characters" which is perceived visually or holistically when identifying or visualising a taxon (Davis and Heywood 1963). The identify of a group emerges in a concrete way in descriptions of the "growth form" or "leaf vein architecture" of a plant. In most groups there is an intimate relationship between "the genotype" and this "identity or core of correlated characters". Cluster analysis forms groups by searching for combinations of correlated characters, which it depicts as clusters, with an accuracy defined as the cophenetic correlation coefficient. Unfortunately, cluster analysis is prone to distort relationships in generation of the phenogram and in the excessive weighting sometimes given to unique characters. This probably explains why *A. callosa* var. *henryi* (the only plant seen with 3 shoots per winter bud) and *A. melanandra* (the smallest leafed "*Leiocarpae*" may emerge more distinctly in this data set compared to the range of plants in the wild, as there are several small-leafed taxa in this Section, not observed in this study, e.g. *A. macrosperma* (Liang 1984).

In a "well-defined" group such as Section *Stellatae*, Series *Perfectae* the "combination or core of correlated characters" may be demonstrated. The correlation matrix for all 80 characters combined (Appendix 4.2) shows that the marker character of this group; "abaxial stellate hairs" is correlated with the following characters:

> long internodes (r^2 = 0.951), wide leaves (r^2 = 0.808); petiole length (r^2 = 0.693), frequency of apex types (r^2 = 0.951), weight of water (r^2 = 0.779); vein types pectinals (r^2 = 0.674), leaf angle re cane (r^2 = 0.742); planar margin orientation (r^2 = 0.682), tertiary vein orientation (r^2 = 0.816), large primary veins (r^2 = 0.742); relative palisade thickness (r^2 = 0.658) and protuberant stomata (r^2 = 0.742).

Thus defining "the core of correlated characters" has diagnosed Section *Stellatae*, Series *Perfectae*. This group is more tightly defined than others in the genus, due to the presence of a distinctive marker character, in conjunction with several other highly correlated characters. Well-defined groups such as this, retain a consistent identity in cluster analysis even when the number and range of organisms being clustered is deliberately reduced (see Figure 3.7, Chapter Three).

Groups which are not as tightly defined, however, are sensitive to variations in the composition of species or characters being clustered; and this explains (in part) some of the inconsistencies which occur during cluster analysis of *Maculatae* and *Strigosae* in Chapter Two.

4.3.2 Taxonomic "range"

Taxonomic groups are also defined in terms of disjunctions in the expressions of important characters. Perception of disjunctions is integral to the process of identification or discrimination. Taxonomic disjunctions or "cut-off points" are partly genetically determined, but the ultimate realisation of characters such as size limits may be environmentally influenced. The use of comparisons between material grown in the wild and under cultivation, (e.g. in a germplasm collection), affords detection of much genotypic variation (Clausen *et al.* 1940). There are indications that the fundamental differences in potentially attainable size between *Leiocarpae* and *Stellatae* are under genetic control, but the adoption of a "bush-like" form suggests that genetic control of plant form in *Actinidia* is not absolute. Detection of "taxonomic range" is more sensitive to statistical variations in the range of taxa sampled within a group and the extent to which exemplars chosen for study are in themselves representative. Although the range of taxa sampled is limited in this study for the genus as a whole, there is reasonable representation of the two geographic and morphological extremes of the group: *Leiocarpae* and *Stellatae*.

Disjunctions in the expression of discrete (yes/no) characters can be easily seen by examination of results tables in this thesis. Well-defined groups, (e.g. *Stellatae*) often emerge as convergences of discontinuities in the expressions of several characters.

Taxonomic treatment of continuous (intergrading) characters such as plant dimensions is greatly aided by the application of discriminant analysis. Making use of the inherent variation expressed by winter shoot characters, has demonstrated their value in classification *per se* and their discriminant efficacy relative to one another. The next step beyond this exploratory investigation would be detailed examination of the ranges of character expression, so that identification keys could be devised.

4.3.3 Use of characters

An aim of this thesis has been exploration of vegetative characters from a wider, more dynamic perspective (Tomlinson, 1984), since many characters are literally "pressed out" of plants deposited in herbaria. Genotypic components in

growth form of *Actinidia* are identifiable at generic and sectional levels, but their application at lower taxonomic levels requires further study. Some species can be identified by their folded (e.g. *A. latifolia*) corrugated (e.g. *A. kolomikta*) or planar (e.g. *A. deliciosa*) leaves. An analysis of growth and morphological characteristics in hybrids such as *A. x fairchildii* (= *A. arguta* x *chinensis*), may provide valuable insight into the heritability of growth form in *Actinidia.*

Observations of juvenile and winter-deciduous shoots demonstrate the need for taxonomists to adopt a temporal more dynamic approach in their mode of data collection. It is important that taxonomists collect data from plants growing in the field, since many useful characters are lost, when samples are taken from whole plants and are pressed and dried for deposition as herbarium voucher specimens. Not only do these "field-characters" assist in identification of *Actinidia*, but they also contribute to the circumscription of these taxa and they also contribute to the resolution of their affinities.

Vegetative morphological characters are inherently more responsive to environmental changes than other structures, but other characters have also evolved in response to environmental agents. Flowers have evolved in response to pollination by wind and insects and many chemical compounds have arisen in response to herbivory.

Solereder (1908) has argued against the use of vegetative characters which are environmentally-determined. However, many of these characters are highly correlated with taxonomically useful "marker" characters and still others have evolved a degree of genetic stability. Leaf anatomy is heritable and predictably consistent under common light or nutritional regimes c.f. Condon thesis, Chapter Two and Gao (1988 - China). Leaf venation patterns are probably more genetically stable than leaf anatomical characters, although both show variation at all taxonomic levels. Such characters are desirable in numerical and conventional taxonomic treatments, because they provide "good taxonomic structure" by contributing information (characters) at all nomenclatural levels.

The use of vegetative characters may even contribute evolutionary information, particularly if a genus is characterised by units which have evolved in different geographic environments, for example, the cool-temperature N.E. Asian or high altitude *Leiocarpae* versus the more warm temperate-subtropical (S.W. Asian or low altitude) *Stellatae* (Liang 1983). It is often subtle combinations of vegetative characters which distinguish varieties (subspecies) of polymorphic and widely distributed species such as *A. arguta* (Li 1952). The subtle gradations in vegetative characters have often led to difficulties in defining taxa (e.g. *A. chinensis* and *A. deliciosa*) in China (Liang 1975, 1982 a,b, Liang and Ferguson 1984).

4.3.4 Evolution of the genus

The application of morphological data in isolation is insufficient to draw evolutionary conclusions about taxa (Bailey 1951). Fortunately, the mucilage data of Redgewell (1983) and the cytotaxonomic data of McNeilage and Considine (1989), suggest that *Leiocarpae* and *Stellatae* are distinctive extremes. The general increase in hair complexity and branching appears to coincide with the increase in chromosome number from *Leiocarpae* (diploids) to *Stellatae*, Series *Perfectae* (diploids and hexaploids), but cytotaxonomic data are far from complete.

To clarify the evolution of the genus as a whole, one would need to examine the entire range of taxa (*ca.* 50 species and as many infraspecific taxa, Ferguson 1990f) and conduct extensive cladistic studies (Jones and Luschinger 1980), preferably using data from diverse sources such as hair morphology, mucilage and phenolic profiles and D.N.A and protein sequencing. Such an approach ought to lead to the creation of "natural" groups. Evidence to date indicates that Sections *Stellatae*, Series *Perfectae* and *Leiocarpae* are likely to be "natural assemblages". Unfortunately, there was insufficient time during the last $2\frac{1}{2}$ years of this investigation to collect chemical data. My study forms part of an integrated program of research instigated by "D.S.I.R Fruit and Trees" in which all aspects of *Actinidia* taxonomy are being investigated.

This exploratory study of *Actinidia* taxonomy is not definitive by any means, but it indicates the value of morphological characters in identifying the plants. Surprisingly, the conservative character "trichome type" has shown major anomalies in the demarcation of major sections of the genus. Sections *Maculatae* and *Strigosae* are demonstrable groupings on geographic grounds, but their validity on other criteria remains uncertain. Appropriate use of genetic resources of *Actinidia* in the wild and under cultivation should lead to a greater understanding of the nature of plant form and how it might be exploited in the development of *Actinidia* cultivars in the future.

ADDENDUM CHAPTER FOUR

Taxonomy

The "apparently anomalous" positions of some taxa in Figure 4.1 ("the combined data set") may now be explained by the misidentification discussed in the addendum to Chapter One.

1. "*A. rufa*" does not cluster with other *Leiocarpae* because it is probably a variety of *A. callosa*, as shown in Figure 4.1.
2. As shown in Figure 4.1, varieties of *A. arguta* group together, so regardless of one's perception of this complex, these taxa are closely related. Both varieties of *A. arguta* are more distinct from each other than *A. chinensis* is to *A. deliciosa*. This might imply the *A. chinensis* has evolved more recently below the species level than *A. arguta*. Some workers (e.g. Bean 1972, Rehder 1951) have even treated infraspecific variants of *A. arguta* as separate species (see discussion, Chapter Three). In both cases, varietal separation has involved morphological as well as chromosomal (polyploidy) differentiation.
3. The application of numerical taxonomy has afforded an objectivity independent of the "assumed identity" of these plants. Although the identity of *A. rufa* was initially accepted at face value in this study, the multivariate analyses did not support this assumption. Cluster analysis was sufficiently sensitive to detect the misclassification before the reason became known. It should also be noted that infraspecific taxa and conspecific genotypes are correctly classified in most of the dendrograms used in this thesis. This too, lends credibility to the multivariate analyses.

Molecular systematics

Recently, Dr R.C. Gardner (Dept. of Cellular and Molecular Biology, University of Auckland) drew my attention to publications arising from his research group on the molecular systematics of *Actinidia*.

1. *Restriction fragment length polymorphisms (R.F.L.P.s)*

   Molecular biologists have developed recombinant D.N.A. methods such as R.F.L.P analysis, which can provide useful insight into systematic relationships of complex groups such as *Actinidia*.

   Basically, helical D.N.A. extracted from *Actinidia* can be ligated with circular D.N.A. from procaryotic vectors. This ligated D.N.A. can be

genomically "engineered" to cut in predictable places, when chemically reacted with suitable restriction-enzymes. Electrophoretic separation and radioactive probing of the "recombinant-D.N.A.", allows one to assess the relatedness of different taxa, by comparing the lengths (in kilobases) of the resultant D.N.A. fragments.

Crowhurst *et al.* (1989) compared the lengths of recombinant D.N.A. fragments arising from four putative parents of *A. deliciosa*. Cladistic analysis (for phylogenetic purposes) showed that *A. deliciosa* was closely related to *A. chinensis*, but only remotely related to *A. latifolia* and *A. eriantha*.

This agrees with results of my phenetic analyses, particularly the dendrogram based on the "combined data set" of 80 morphological characters from winter and summer shoots (Figure 4.1). I recently sent a copy of this dendrogram to Dr R.C. Gardner, who intends to use this tree as an hypothesis for testing the relatedness of *Actinidia* taxa in the D.S.I.R. *Actinidia* germplasm collection.

2. *Genomic (D.N.A. repeat) sequences*

Analysis of "moderately repetitive D.N.A. base sequences" (Crowhurst and Gardner 1991) shows that *A. deliciosa* shares a 50 kb "repeat-sequence" with *A. deliciosa* var. *chlorocarpa*, but not with *A. chinensis* or eight other *Actinidia* species. This is surprising in view of the morphological differences between *A. chrysantha* and *A. deliciosa*. However, it does suggest that kiwifruit (a hexaploid) is an allopolyploid species. This finding is not at variance with other morphological evidence.

References (Chapter 4 Addendum) : Not in general ref. list, pp. 230-241

Crowhurst, R.N., Lints, R., Atkinson, R.G. and Gardner, R.C. (1990)
Restriction fragment length polymorphisms in the genus *Actinidia* (Actinidiaceae).
Pl. Syst. Evol. 172: 193-203.

Crowhurst, R.N. and Gardner, R.C. (1991)
A genome-specific repeat sequence from kiwifruit (Actinidia *deliciosa* var. *deliciosa*).
Theor. Appl. Genet. 41: 71-78.

ACKNOWLEDGEMENTS

I would like to thank the following people for competent technical assistance:

Neil Andrews (S.E.M.), Reijel Gardiner (Histology);

Manfred Ingerfeld (T.E.M.), Lee Leonard (Drawings), and

Derek Stewart, Dougal Holmes (Photography) and Beverley Bristowe for patient and careful typing of the work.

Nancy Goh for typing the Plate captions, and to Jane Chambers for her assistance in typing some of the tables.

I appreciate the scientific advice and/or assistance given by my friends and colleagues, particularly:

Drs. Ilse Breitwieser (Taxonomy), Chris Frampton (Numerical taxonomy and multivariate analysis; Ian Daniel (Taxonomy and general Botany), and Jo Ward (Cluster analysis).

Thanks are extended to Mr Bill Sykes (Botany Division, D.S.I.R., Lincoln) for access to herbarium specimens of *Actinidia* collected in Asia; to Drs. Ross Ferguson and Mark McNeilage for collections of live material from the D.S.I.R. *Actinidia* germplasm collection, at Auckland and Te Puke.

I gratefully acknowledge the constructive guidance and criticism given by my supervisor:

Dr B.A. Fineran (P.A.M.S. Dept., University of Canterbury),

associate supervisor:

Dr B.G. Butterfield (also of the P.A.M.S. Dept.),

and external associate supervisor:

Dr A.R. Ferguson (D.S.I.R. Fruit and Trees).

I am grateful for financial support provided by my parents and the University Grants Committee during the course of this thesis.

REFERENCES

An, H.-X., Cai, D.-R., Wang, J.-R., and Qian, N.-F. (1983) [Investigations on early embryogenesis on *Actinidia chinensis* Planch. var. chinensis]. *Acta. Bot, Sin.* **25**:99-103, + 2 pls.

Anon. (1973) Die knospen der Chinesischen *Actinidia*: verbogen und geborgen. *Mitteilungen aus dem Botanischen Garten St. Gallen*, Marz 1973/22 Jahrgang Nr.3.

Anon. (1979) [The *Actinidia* genus.] pp.193-209 *In*: *Chinese Fruit-Tree Taxonomy.* (Zhongguo Guoshu Fenliexue) Yu Dejun (Ed.) 421 pp.

Antcliff, A.J. & Webster, W.J. (1955) Studies on the sultana vine. I. Fruit bud distribution and bud burst with reference to forecasting potential crop. *Aust. J. Agr. Res.* **6**: 565-588.

Antcliff, A.J., Webster, W.J. & May, P. (1958) Studies on the sultana vine. VI. The morphology of the cane and its fruitfulness. *Aust. J. Agr. Res.* **9**: 328-338.

Astridge, S.J. (1975) Cultivars of Chinese gooseberry (*Actinidia chinensis*) in New Zealand. *Econ. Bot.* **29**: 357-360.

Bailey, I.W. (1951) The use and abuse of anatomical data in the study of phylogeny and classification. *Phytomorphology* **1**: 67-69.

Bean, W.J. (1972) Taylor, G.S. (Ed.). *Trees and shrubs hardy in the British Isles*, 4 vols. Vol. I, A-C. 8th Rev. Edition. John Murray. 845 pp.

Beauvisage, L. (1920) Contribution à l'*étude anatomique de la famille des Ternstroemiacées.* D.Sc. Natur. Thesis Poitiers, Arrault et Cie Tours. 470 pp.

Behnke, H.-D. (1981) Sieve-element characters. *Nord. J. Bot.* **1**: 381-400.

Berestova, G.N. (1970) [Some varieties of *Actinidia* and *Schizandra chinensis* in the southern parts of Khabarovsk region]. *Sbornik trudov aspirantov: molodykh nauchnykh sotrundnikov* **17**: 482-486.

Blanchet, P. (1989) Description et comportement d'espèces d' *Actinidia* à fruits glabres dans le Sud-Ouest de la France. *Fruits* 44 (10): 543-552.

Breitwieser, I. (1990) *Leaf anatomy and chemotaxonomy in Gnaphaliinae (Inulae-Compositae).* Ph.D thesis (Botany) Dept. of Plant and Microbial Sciences, University of Canterbury + 18 pls, 195 pp.

Brothers, P.M. (1988) The effect of position on bud burst and shoot development in *Actinidia deliciosa* (A. Chev.) C.F. Liang *et* A.R. Ferguson. M.Sc. Thesis (Botany), University of Auckland, N.Z. 126 pp.

Brundell, D.J. (1975)a Flower development of the Chinese gooseberry (*Actinidia chinensis* Planch.). I. Development of the flowering shoot. *N.Z. J. Bot.* **13**: 473-83.

Brundell, D.J. (1975)b Flower development of the Chinese gooseberry (*Actinidia chinensis* Planch.). II. Development of the flower bud. *N.Z. J. Bot.* **13**: 485-496.

Brundell, D.J. (1975)c Quantitative aspects of flowering in the Chinese gooseberry *Actinidia chinensis* Planch.). *N.Z. J. Agr. Res.* **18**: 371-374.

Brundell, D.J. (1975)d Effect of defoliation, shading, and tipping of shoots on flower bud development and vegetative growth of the Chinese gooseberry (*Actinidia chinensis* Planch.) *N.Z. J. Agr. Res.* **18**: 365-370.

Busgen, M. (1929) *The structure and life of forest trees* (3rd Rev. Ed.). Chapman and Hall Ltd., London. 436 pp.

Clark, C.J., Smith, G.S. and Walker, G.D. (1987) The form, distribution and seasonal accumulation of Calcium in kiwifruit leaves. *New Phytol* **105**: 477-486

Clausen, J., Keck, D.D. and Hiesey, W.M. (1940) Experimental Studies on the Nature of Species. I. Effect of Varied Environments on Western North America Plants. *Carnegie Inst. Washington Publ.* No. 520.

Clothier, B., Snow, V., Green, S., Sauer, T., Nicholson, H., Gandar, P., Trought, M., Hughes, K and Lok, J. (1986) Water economy of kiwifruit vines, pp.16-19. *In: Proceedings of the N.Z.K.A. National Research Conference* (Rotorua) July 8, 1986. *New Zealand Kiwifruit*, special publication No. 1.

Clothier, B.E., Hughes, K.A., Gandar, P.W., McAneney, K.J., Green, S.R. and Kerr, J.P. (1988) Soil-water, roots and water-use, pp.18-21. *In : Proceedings of the N.Z.K.A. National Research Conference*, (Rotorua) July 18-19, 1988. *New Zealand Kiwifruit*, special publication No. 2.

Condon, J.M. and Fineran, B.A. (1989) Distribution and organisation of articulated laticifers in *Calystegia silvatica* (Convolvulaceae). *Bot. Gaz.* **150**: 289-302.

Corbet, S.A., Chapman, H. and Saville, N. (1988) Vibratory pollen collection and flower form: bumble-bees on *Actinidia*, *Symphytum*, *Borago* and *Polygonatum*. *Functional Ecology* **2**: 147-155.

Cronquist, A. (1981) *An integrated system of classification of flowering plants.* Columbia University Press, New York. 1262 pp.

Darwin, C. (1875) *The movements and habits of climbing plants.* (2nd Rev. Ed.). J. Murray, London. 208 pp.

Davis, P.H. and Heywood, V.H. (1963) *Principles of angiosperm taxonomy.* Oliver and Boyd, Edinburgh and London. 556 pp.

Dawes, S.N. (1977) Breeding and selection of kiwifruit pp.1-11. *In : Proceedings Kiwifruit Seminar*, Tauranga, 7 September, 1977 [Tauranga]:[New Zealand] Ministry of Agriculture and Fisheries. 66 pp.

Dean, J.M. and Smith, A.P. (1978) Behavioral and morphological adaptations of a tropical plant to high rainfall. *Biotropica* **10**: 152-154.

Dilcher, D.L. (1974) Approaches to the identification of angiosperm leaf remains. *Bot. Rev.* **40**:1-157.

Dunac, F.D. (1899) Contribution à l'étude du genre *Actinidia* (Dilléniacées). *C.R. Acad. Sci.* (Paris) **128**: 1598-1601.

Dunn, S.T. (1908) A botanical expedition to Central Fukien. *J. Linn. Soc.* Bot., (Lond.) **38**: 350-373.

Dunn, S.T. (1911) A revision of the genus *Actinidia*, Lindl. *J. Linn. Soc.* Bot., (Lond.) **39**: 394-410.

Esau, K. (1965) *Anatomy of seed plants* (2nd Ed.) New York, London and Sydney, 767 pp.

Esau, K. (1965) *Plant anatomy* (2nd Ed.) John Wiley and Sons Inc., New York/London/Sydney. 767 pp.

Esau, K. (1976) *Anatomy of seed plants* (2nd Ed.) John Wiley and Sons, New York/Santa Barbara/London/Sydney/Toronto. 550pp.

Fahn, A. (1979) *Secretory tissues in plants.* Academic Press, London. 302pp.

Fahn, A. (1982) *Plant anatomy* (3rd Ed.) Pergamon Press, Oxford, New York, Toronto, Sydney, Paris, Frankfurt. 544pp.

Fairchild, D. (1927) The fascination of making a plant hybrid: being a detailed account of the hybridisation of *Actinidia arguta* and *Actinidia chinensis. J. Hered.* **18** : 49-62.

Feder, N. and O'Brien, T.P. (1968) Plant microtechnique: some principles and new methods. *Amer. J. Bot.* **55** : 123-142.

Feist, A. (1887) Ueber die Schutzeinrichtungen der Laubknospen Dicotyler Laubbaume. *Deutsche Akademie der Naturforscher zu Halle Nova Acta.* **51** : 303-344.

Ferguson, A.R. (1983) E.H. Wilson, Yichang, and the Kiwifruit. *Arnoldia,* **43** : 24-35.

Ferguson, A.R. (1984) Kiwifruit : a botanical review. *Hortic. Reviews* **6** : 1-64.

Ferguson, A.R. (1990a) *Actinidia, In:* Moore, J.N., Ballington, J.R., (eds), *Genetic resources of temperate fruit and nut crops.* I.S.H.S., Wageningen (?), in press.

Ferguson, A.R. (1990b) Botanical nomenclature: *Actinidia chinensis, Actinidia deliciosa,* and *Actinidia setosa,* pp36-57 + 2 pls. *In:* Warrington, I.J., Weston, G.C. (eds). *Kiwifruit: science and management.* Ray Richards Publisher in association with the New Zealand Society for Horticultural Science, Auckland, 576pp.

Ferguson, A.R. (1990c) Kiwifruit management. pp.472-505 *In:* Galletta, G.J., Himelrick, D.G. (eds), *Small fruit crop management.* Prentice Hall, Englewood Cliffs xxii+, pp.

Ferguson, A.R. (1990d) Nuove cultivar ed altre specie di *Actinidia. Frutticoltura* 52 (10) : 9-16.

Ferguson, A.R. (1990e) Stems, branches, leaves and roots of the kiwifruit vine. pp.58-70 *In:* Warrington, I.J., Weston, G.C. (eds), *Kiwifruit: science and management.* Ray Richards Publisher in association with the New Zealand Society for Horticultural Science, Auckland, 576 pp.

Ferguson, A.R. (1990f) The genus *Actinidia,* pp.15-35 + 5 pls. *In:* Warrington, I.J., Weston, G.C. (eds), *Kiwifruit : science and management.* Ray Richards Publisher in association with the New Zealand Society for Horticultural Science, Auckland. 576 pp.

Ferguson, A.R. and Bollard, E.G. (1990) Domestication of the Kiwifruit. pp.165-246 + 3 pls. *In:* Warrington, I.J., Weston, G.C. (eds), *Kiwifruit : science and management.* Ray Richards Publisher in association with the New Zealand Society for Horticultural Science, Auckland. 576pp.

Ferguson, A.R., and Davison, R.M. (1986) *Actinidia deliciosa* pp.1-14 *In:* Halevy, A.H. (ed.) C.R.C. Handbook of Flowering, **vol.5**, C.R.C. Press Inc, Boca Raton, Florida. 414pp.

Fineran, B.A. (1978) Freeze-etching, pp.279-341 in J.L. Hall (ed.) *Electron microscopy and cytochemistry of plant cells.* Elsevier/North-Holland Biomedical Press, Amsterdam. 444pp.

Fineran, B.A. and Condon, J.M. (1988). The stabilisation of latex in laticifers of the Convolvulaceae: application of freezing methods for scanning electron microscopy. *Can. J. Bot.* **66**: 1217-1226.

Fineran, B.A. and Johnston, (1974) Adaptation of a rotary microtome for sectioning with glass knives. *J. Microsc.* **100** : 337-339.

Fisher, R.A. (1936) The use of multiple measurements in taxonomic problems. *Ann. Eugenics* **7** : 179-188.

Florek, (1951)a Sur la liason et la division des points d'un ensemble fini. *Colloqium Math.* **2**: 282-285 (not seen).

Florek, (1951)b Taksonomia Wroclawska. *Przegl. Antropol.* 17: 193-211 (not seen).

Frampton, C.M. (1988) *Multivariate numerical analyses of Raoulia subgenus Raoulia.* Ph.D thesis (Botany) Dept. of Plant and Microbial Sciences, University of Canterbury, N.Z. 117pp.

Fujita, T. (1935) [On the anatomy and greening of variegation in *Saururus loureirii* Decne and *Actinidia polygama* Planch.]. *Botany and Zoology (Tokyo)* **3**: 737-748.

Gao, Z.-M. (1988) [Anatomical studies of the main vegetative organs in the *Actinidia* of Henan.]. *Guihaia* **8** : 153-164.

Gilg, E. (1893) Dilleniaceae. pp.100-128. *In:* H.[G.A.] Engler and K.[A.E.] Prantl (eds). *Die natürlichen Pflanzenfamilien, nebst ihren Gattungen und* wichtigen Arten, inbesondere den Nutzpflanzen. Teil 3, Abt.6, Lief 80. pp. 100-128. Verlag Wilhelm Engelmann, Leipzig.

Givnish, T.J. (1987) Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytologist* 106 (Suppl.): 131-160.

Givnish, T.J. and Vermeij, G.J. (1976) Sizes and shapes of liane leaves. *Amer. Natur.* 110 : 743-778.

Gower, J.C. (1971) A general coefficient of similarity and some of its properties. *Biometrics* **27**: 857-871.

Gui, Y.-L. (1981) [Comparative morphological observations of two varieties of *Actinidia chinensis* Planch.]. *Acta Phytotaxonomica Sinica* **19**(3): 304-307.

Guy, C.L. (1990) Cold acclimation and freezing stress tolerance: role of protein metabolism. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* 41: 187-223.

Halle, F., Oldeman, R.A.A. and Tomlinson, P.B. (1978) *Tropical trees and forests.* (An Architectural Analysis). Springer-Verlag; Berlin, Heidelberg, New York. 441 pp.

Harman, J. (1981) Kiwifruit testing for maturity: use of index. New Zealand Ministry of Agriculture and Fisheries. Media Services. *AgLink* HPP 213, 1pp.

Harvey, C.F., Fraser, L.G., Pavis, S.E. and Considine, J.A. (1987) Floral biology of two species of *Actinidia* (Actinidiaceae). I. The stigma, pollination and fertilisation. *Bot. Gaz.* **148** : 426-432.

Harvey, C.F. and Fraser, L.G. (1988) Floral biology of two species of *Actinidia* (Actinidiaceae). II. Early embryology. *Bot. Gaz.* **149** : 37-44.

Hewett, E.W. & Young, K. (1981) Critical freeze damage temperatures of flower buds of kiwifruit (*Actinidia chinensis* Planch.) *N.Z. J. Agr. Res.* 24: 73-75.

Heywood, V.H. (1971) Scanning electron microscopy in the study of plant materials *Micron.* **1** : 1-14.

Hickey, L.J. (1973) Classification of the architecture of dicotyledonous leaves. *Amer. J. Bot.* **60** : 17-33.

Hickey, L.J. (1979) A revised classification of the architecture of dicotyledonous leaves, pp. 25-39. *In:* Metcalfe, C.R. and Chalk, L. (eds), *Anatomy of the dicotyledons* (2nd Ed.) **vol I.** (Systematic anatomy of the leaf and stem, with a brief history of the subject). Clarendon Press, Oxford + 18 pls, 276 pp.

Hickey, L.J. and Wolfe, J.A. (1975) The bases of angiosperm phylogeny : vegetative morphology. *Ann. Missouri Bot. Gard.* **62** : 538-589.

Hildebrand, F. (1883) Ueber einige Fälle verborgenen Zweigknospen. *Botanisches Centralblatt* 13: 207-212.

Hitzemann, C. (1886) Beiträge zur vergleichenden Anatomie der Ternstroemiaceen, Dilleniaceen, Diptocarpaceen und Chlaenaceen. Ph.D Thesis, Univ. Kiel. Giebel and Oehlschlägel, Osterode a.H.

Hopping, M.E. (1985) Spray pollination: progress and likely economics. *Kiwifruit Proceedings.* Ruakura Horticultural Conference 1985.

Isebrands, J.G. and Larson, P.R. (1980) Ontogeny of major veins in the lamina of *Populus deltoides* Bartr. *Amer. J. Bot.* **67** : 23-33.

Jaccard (1908) Nouvelles recherches sur la distribution florale. *Bull. Soc. Vaud. Sci. Nat.* 44: 223-270.

Jackson, D.I. (1986) *Temperate and subtropical fruit production.* Butterworths Horticultural Books: Wellington, N.Z. 294 pp.

Jackson, D.I. & Sweet, G.B. (1972) Flower initiation in temperate woody plants. *Hortic. Abstr.* 42: 9-25.

John, J. and Kolbe, K.-P. (1980) The systematic position of the "Theales" from the viewpoint of Serology. *Biochemical Systematics and Ecology* **8** : 241-248.

Jones, S.B. and Luchsinger, A.E. (1980) *Plant systematics* (2nd Ed.). McGraw-Hill Book Company, New York etc. 512pp.

Kaplan, D.R. (1971) Leaf (botany) pp. 251-254, *In:* McGraw-Hill *Yearbook of Science and Technology.*

Kaplan, D.R. (1973) The monocotyledons : their evolution and comparative biology VII. The problem of morphology and evolution in the monocotyledons. *Quart. Rev. Biol.* **48** : 437-457.

Kolbasina, E.I. (1963) [A contribution to the ecology of wild *Actinidia kolomikta* on Sakhalin Island]
Tr. Sakhalin.Kompleksn. Nauchno-Issled. Inst. Akad. Nauk SSSR Sib. Odt. **13**: 71-78.

Kolbe, P.-K,. and John, J. (1980) Serology and systematics of the Ebenales and the Theales. *Biochemical Systematics and Ecology* **8** : 249-256.

Krause, C.R. (1978) Identification of four red maple cultivars with scanning electron microscopy. *HortScience* **13** : 586-588.

Krause, C.R. (1982) Differentiation of black and sugar maple cultivars with scanning electron microscopy. *J. Amer. Soc. Hort. Sci.* **107** : 186-188.

Krüssmann, G. (1976) 1984 *Actinidia* pp110-115. In: *Manual of cultivated broad-leaved trees and shrubs* 3 vols., Vol. I, A-D B.T. Batsford Ltd., London. 448 pp.

Küster, E. (1928) Beiträge zur Kenntnis der panaschierten Gehölze XVIII-XXII. *Mitteilungen der Deutschen Dendrologischen Gesellschaft* **40** : 258-267.

Küster, E. (1933) XXXVII. Anthozyanbildung an panaschierten Pflanzen *Mitteilungen der Deutschen Dendrologischen Gessellschaft* **45** : 288-290.

Lawrence, George H.M. (1951) *Taxonomy of vascular plants.* Macmillian Company: New York, 823pp.

Lechner, S. (1915) Anatomische Untersuchungen über die Gattungen *Actinidia, Saurauia, Clethra* und *Clematoclethra* mit besonderer berücksichtigung ihrer Stellung im System. *Bot. Zentralbl. (Beih).* **32** : 431-467.

Lees, H.M.N. (1982) Kiwifruit *(Actinidia chinensis)* Hayward variety increases in fruit size from March to June, during three seasons. *The Orchardist of New Zealand.* **55** : 72-74.

Lemon, C.W. (1988) The root system of *Actinidia deliciosa* (A. Chev.) C.F. Liang *et.* A.R. Ferguson var. *deliciosa* (kiwifruit vine). M.Sc. thesis (Botany), University of Auckland, 104 pp.

Lersten, N.R. and Curtis, J.D. (1982) Hydathodes in *Physocarpus* (Rosaceae: Spiraeoideae). *Canad. J. Bot.* **60** : 850-855.

Li H.-L. (1952) A taxonomic review of the genus *Actinidia*. *J. Arnold. Arbor. Harvard Univ.* 33: 1-61.

Li R.-G., Liang, M.-Y., Hunag, C.-G., Hu, S.-H. and Huang, Z.-F. (1987) [Observation and analysis of *Actinidias* planted in Guilin germplasm orchard.] *Guihaia* 7 : 325-331

Liang, C.-F. (1975) [Classification of *Actinidia chinensis* Planch.] *Acta Phytotaxonomica Sinica* 13 : 32-35.

Liang, C.-F. (1980) [The classification of Chinese gooseberries in China]. *Guihaia* 1: 30-45.

Liang, C.-F. (1982a) [An addition to the infraspecific taxa of *Actinidia chinensis* Planch.] *Acta Phytotaxonomica Sinica* 20 : 101-104.

Liang, C.-F. (1982b) [New taxa of the genus. *Actinidia* Lindl.] *Guihaia* 2 : 1-6.

Liang, C.-F. (1983) [On the distribution of *Actinidia Guangxi Zhiwu*.] *Guihaia* 3(4): 229-248.

Liang, C.-F. (1984) [*Actinidia*] in Feng, K.-M. (ed.) *Flora Reipublicae Popularis Sinicae* [Beijing] Science Press **vol. 49(2)**, pp. 196-268, diagnoses 324-329. [Translation provided by Professor Liang Chou-Fen].

Liang, C.-F. & Ferguson, A.R. (1984) [Emendation of the Latin name of *Actinidia chinensis chinensis* Pl. var. *hispida* C.F. Liang]. *Guihaia* 4: 181-182.

Liang, C.-F. & Ferguson, A.R. (1986) Short communication: The botanical nomenclature of the kiwifruit and related taxa. *N.Z.J. Bot.* 24: 183-184.

Liao, J.-S. and Wang, T.-C. (1984) [A preliminary investigation on the distribution and ecological characteristics of Chinese *Actinidia* in Fujian.] *Journal of Fujian Agricultural College* 13 : 291-297.

Lindley, J. (1836) A natural system of botany; or a systematic view of the organization, natural affinities, and geographical distribution, of the whole vegetable kingdom...(2nd ed.) Longman, London.

Lionakis, S.M. & Schwabe, W.W. (1984a) Bud dormancy in the kiwi fruit *Actinidia chinensis* Planch. *Ann. Bot.* (N.S., London) 54: 467-484.

Lionakis, S.M. and Schwabe, W.W. (1984b) Some effects of daylength, temperature and exogenous growth regulator application on the growth of *Actinidia chinensis* Planch. *Ann Bot.* 54 : 485-501.

Lubbock, J. (1899) *On buds and stipules*. Kegan, Paul, Trench, Trübner & Co. Ltd., London, (+ 4 Pls.), 239 pp.

Martin, J.T. and Juniper, B.E. (1970) *The cuticles of plants*, Edward Arnold Ltd., Edinburgh, 347pp.

Marty, M.F. (1978) Cytochemical studies on G.E.R.L., provacuoles and vacuoles in root meristematic cells of *Euphorbia*. *Proc. Nat. Acad. Sci.* (U.S.A.) 75 : 852-856.

Martyn, J. and Hopping, M. (1988) How to identify superior males. *N.Z. Kiwifruit* No.42 (Feb. 1988) : p 29.

McAneney, K.J. and Judd, M.J. (1983) Observations on kiwifruit (*Actinidia chinensis* Planch.) root exploration, root pressure, hydraulic conductivity and water uptake. *N.Z.J. Agr. Res.* **26** : 507-510.

McAneney, K.J., Judd, M.J. and Trought, M.C.T. (1984) Wind damage to kiwifruit (*Actinidia chinensis* Planch.) in relation to windbreak performance. *N.Z.J. Agr. Res.* **27** : 255-263.

McNeilage, M.A. & Considine, J.A. (1989) Chromosome studies in some *Actinidia* taxa and implications for breeding. *N.Z.J. Bot.* **27**: 71-81.

Metcalfe, C.R. (1983) Anomalous structure. Chapt. 2. pp. 52-63. *In* : Metcalfe, C.R. and Chalk, L. (eds.) *Anatomy of the dicotyledons* (2nd Ed.) **Vol.II** (Wood structure and conclusion of the general introduction). Clarendon Press, Oxford + 11 pls., 297pp.

Metcalfe, C.R. & Chalk, L. (1950) *Anatomy of the dicotyledons.* 2 vols, Clarendon Press, Oxford. 1500pp.

Michurin, I.V. (1949) *Selected works.* Foreign Languages Publishing House, Moscow, 496 pp.

Morgan, D.C., Stanley, C.J. and Warrington, I.J. (1985) The effects of simulated daylight and shade-light on vegetative and reproductive growth in kiwifruit and grapevine. *Journal of Horticultural Science* **60** : 473-484.

Mouat, H.M. (1958) New Zealand varieties of Yangtao or Chinese gooseberry. *N.Z.J. Agr.* **97** : 161, 163, 165.

Palmer-Jones, T. and Clinch, P.G. (1975) Honey bees essential for kiwifruit pollination. *The Orchardist of New Zealand* **48** : p.347.

Payne, W.W. (1978) A glossary of plant hair terminology. *Brittonia* **30** : 239-255.

Perrin, A. (1971) Presence de <<cellules de transfert>> au sein de l'épithème de quelques hydathodes. *Z. Pflanzenphysiol.* Bd. **65** : 39-51.

Perrin, A. and Zandonella, P. (1971) Présence d'invaginations nucléaires dans les cellules de quelques nectaires floraux et hydathodes. *Planta* (Berl.) **96** : 136-144.

Philipson, W.R. (1974) Ovular morphology and the major classification of dicotyledons. *Bot. J. Linn. Soc. (Lond.)* **68** : 89-108.

Philipson, W.R. (1977) Ovular morphology and the classification of dicotyledons. *Plant Syst. Evol. (Suppl)* **1** : 123-140.

Philipson, W.R. and Molloy, B.P.J. (1990) Seedling, shoot and adult morphology of New Zealand conifers. The genera *Dacrycarpus, Podocarpus; Dacrydium* and *Prumnopitys. N.Z.J. Bot.* **28** : 73-84.

Planchon, J.E. (1847) Sur la nouvelle famille des Cochlospermées. *Lond. J. Bot.* **6** : 294-311.

Poyarkova, A.I. (1949) Actinidiaceae van Tiegh, p138-147. *In*: B.K. Shishken (Ed.) Malvales, Parietales, Myrtiflorae. *Flora of the USSR*, XV (Transl. of Flora URSS XV: 185-197) Israel Program for Scientific Translations, Jerusalem.

Pray, T.R. (1955) Foliar venation of angiosperms. II. Histogenesis of the venation of *Liriodendron*. *Amer. J. Bot.* 42 : 18-27.

Pray, T.R. (1963) Origin of vein endings in angiosperm leaves. *Phytomorphology* 13 : 60-81.

Pulawska, Z. (1965) Correlations in the development of the leaves and leaf traces in the shoot of *Actinidia arguta* Planch. *Acta Societatis Botanicorum Poloniae* 34 : 697-712.

Radford, A.E., Dickison, W.C., Massey, J.R, and Bell, C.R. (1974). *Vascular plant systematics*, Harper and Row, New York, 891pp.

Radlkofer, L. (1875) *Serjania*, Sapindac earum genus monographice description. *München : Kön, bayer. Akad. JB*, 3 : 430 (Not seen, cited in Solereder 1908).

Redgwell, R.J. (1983) Composition of *Actinidia* mucilage. *Phytochemistry* 22: 951-956.

Rehder, A. (1951) *Manual of cultivated trees and shrubs (hardy in North America)*. New York, The Macmillan Company, 996 pp.

Robards, A.W. (1978) An introduction to techniques for scanning electron microscopy of plant cells. (Chapt. 7), pp. 343-415. *In* : Hall, J.L. (ed.), *Electron microscopy and cytochemistry of plant cells.* Elsevier/North-Holland Biomedical Press, Amsterdam, 444pp.

Robards, A.W. and Sleytr, U.B. (1985) Low temperature methods in biological electron microscopy, pp343-415. *In :* Glauert, A.M. (ed.) *Practical methods in electron microscopy* **Vol.10**, Elsevier, Amsterdam, 551pp.

Rohlf, F.J. (1970) Adaptive hierarchical clustering schemes. *Systematic Zool.* 19 : 58-82.

Sakai, A. & Larcher, W. (1987) *Frost survival of plants.* (Ecological Studies series, 62), 321 pp.

Sale, P. (1983) The value of stubs and spurs in kiwifruit management. *The Orchardist of New Zealand* 56 : p. 362.

Sale, P.R. (1985) *Kiwifruit culture.* (2nd Edition). (Ed.) D.A. Williams. Government Printing Office, Wellington, 96 pp.

Sargent, C.S.S. (1894a) *Forest flora of Japan* (Notes on the forest flora of Japan). Houghton, Mifflin and Company : Boston and New York; The Riverside Press, Cambridge, 93pp.

Sargent, C.S.S. (1894b) *Manual of the trees of North America* (exclusive to Mexico) (2nd ed.,) [1921]. Constable and Co. Ltd., London, 910pp.

Schmid, R. (1978) Reproductive anatomy of *Actinidia chinensis* (Actinidiaceae). *Bot. Jahrb. Syst.* **100** : 149-195.

Seal, A. and McNeilage, M. (1988) New red and green fleshed *Actinidia. New Zealand Kiwifruit* **42** (Feb. 1988) : 9.

Siebold, P.F. de; Zuccarini, J.G. (1843) Plantarum, quas in Japonia collegit Dr. Ph. Fr. de Siebold, genera nova *Abhandlung der Mathematisch-Physikalischen Classe der Könglich Bayerischen Akademie der Wissenschaften* **3**: 717-749 + 5 pls.

Sneath, P.H.A. (1957) The application of computers to taxonomy. *J. Gen. Microbiol.* **17**: 201-226.

Sneath, P.H.A. & Sokal, R.R. 1973 *Numerical taxonomy*. Freeman, San Francisco, 573pp.

Sokal, R.R. & Michener, C.D. (1958) A statistical method for evaluating systematic relationships. *Univ. Kansas Sci. Bull.* **38** : 1409-1438.

Sokal, R.R. & Rohlf, F.J. (1962) The comparison of dendrograms by objective methods. *Taxon* **11** : 33-40.

Solereder, H. (1908) *Systematic anatomy of the dicotyledons*, (Rev. Ed.) Transl. by Boodle, L.A. and Fritsch, F.L., 2 vols., Clarendon Press, Oxford, 1182pp.

Spicer, R.A. (1986) Pectinal veins: a new concept in terminology for the description of dicotyledonous leaf venation patterns. *Bot. J. Linn. Soc.* (Lond.) **93** : 379-388.

Spurr, A.R. (1969) A low-viscosity epoxy resin embedding medium for electron microscopy. *J. Ultrastruc. Res.* **26** : 31-43.

Stace, C.,A. (1965) Cuticular studies as an aid to plant taxonomy. *British Museum of Natural History Bulletin, Botany* **Vol. 4** : 3-78 + 5 pls.

Stanley, C.J., McPherson, H.G., Warrington, I.J., Jansson, D.M. (1988) Spring temperature effects on budbreak and flowering in kiwifruit, p12-14. *In*: Biennial Report - Plant Physiology Division, D.S.I.R, 78 pp.

Stapf, O. (1926) *Actinidia kolomikta* (East Asia). *Curtis' Botanical Magazine* **151** ("1925") Tab. 9093.

Stearn, W.T. (1966) *Botanical latin.* Thomas Nelson and Sons Ltd., London and Edinburgh, 566pp.

S.Y.S.T.A.N.Z. (1962) Systematics Association Committee for Descriptive Terminology. Terminology of simple symmetrical plane shapes (Chart 1). *Taxon* **11** : 145-156, 245-247.

Tomlinson, P.B. (1984) Vegetative morphology - some enigmas in relation to plant systematics, pp49-66. *In* : Heywood, V.H. and Moore, D.M. (eds.) *Current concepts in plant taxonomy.* Systematics Association Special Volume No. 25, 430pp. Academic Press, London, Orlando, etc.

Tregear, T.R. (1980) *China, a geographical survey.* Hodder and Stoughton, London and Sydney, 372 pp.

U.P.O.V. (1981) [International Union for the Protection of New Varieties of Plants (U.P.O.V)]. Draft guidelines for the conduct of tests for distinctness, homogeneity and stability. KIWI FRUIT ACTINIDIA KIWI (*Actinidia chinensis* Pl.).

Van Tieghem, P. (1899) Sur les genre Actinidie et Sauravie considérés comme types d'une famille nouvelle, les Actinidiacées. *Ann. Sci. Nat. Bot. Biol. Vég. Sér.* 8, 10 : 137-140.

Vasiliev, N.G. (1961) [A rare example of *Actinidia*]. *Nature* 5 : 115-116.

Vegis, A. (1964) Dormancy in higher plants. *Ann. Rev. Plant. Physiol.* 15: 185-224.

Vijayaraghavan, M.R. (1965) Morphology and embryology of *Actinidia polygama* Franch. & Sav. and systematic position of the family Actinidiaceae. *Phytomorphology* 15 : 224-235.

Vince-Prue, D. (1985) Chapt. 9, Photoperiod and hormones pp 308-364. *In*: *Hormonal regulation of development III. Role of environmental factors.* (Eds) Pharis, R.P. and Reid, D.M. Encyclopedia of Plant Physiology New Series Vol. 11. 887 pp. Springer-Verlag; Berlin, Heidelberg, New York, Tokyo.

Vorobiev, D.P. (1939) [Review of far eastern species of genus *Actinidia.*] Trudy Gornotaezhnoi stantsii Dal'nevostochnyi Filial Akademii Nauk SSSR, Valdivostock 3: 5-38.

Warrington, I.J. (1990) Areas and trends of kiwifruit production in New Zealand and around the world. pp511-525. *In*: Warrington, I.J., Weston, G.C. (eds.) *Kiwifruit: science and management.* Ray Richards, Publisher, in association with the New Zealand Society for Horticultural Science, Auckland, 576 pp.

Weiser, C.J. (1970) Cold resistance injury in woody plants. *Science* 169: 1269-1278.

Westwood, M.N. (1988) *Temperate zone pomology.* (Rev. Ed.) Timber Press, Portland, Oregon. 428pp.

Wetmore, R.H. and Garrison, R. (1959) The growth and organisation of internodes. pp.827-832 *In*: *Recent advances in botany*, Vol. I. Proceedings of the IX Botanical Congress, Montreal 1959.

White, J. (1986a) Morphology of the fruit hairs in cultivars of *Actinidia deliciosa* var. *deliciosa*, *Actinidia eriantha*, and *Actinidia rufa* *N.Z.J.Bot.* 24 : 415-423.

White, J. (1986b) Ontogeny and morphology of ovarian and fruit hairs in kiwifruit. *N. Z. J. Bot.* 24 : 403-414.

Wilkinson, H.P. (1979) The Plant Surface (Mainly leaf); Part II: Hydathodes pp.117-125. *In* : Metcalfe, C.R. and Chalk, L. (1979) *Anatomy of the dicotyledons* (2nd Ed.) Vol.I (Systematic anatomy of leaf and stem with a brief history of the subject). Clarendon Press, Oxford + 18 pls, 276pp.

Wratt, G.S. & Smith, H.C. (Eds) (1983) *Plant breeding in New Zealand.* Butterworths N.Z. (Ltd.) in association with the D.S.I.R, Wellington, N.Z., 309 pp.

Yerex, D. and Haines, W. (1983) *The kiwifruit story.* Agricultural Publishing Associates Ltd., Masterton, N.Z. 96pp.

Zhang Jie & Thorp, T.G. (1986) Morphology of nine pistillate and three staminate New Zealand clones of kiwifruit (*Actinidia deliciosa* (A. Chev.) C.F. Liang et A.R. Ferguson var. *deliciosa*). *N.Z.J. Bot.* 24: 589-613.

Zhu Hongyuan (1983) Zhonghua mihoutao zaipei. Shanghai, Shanghai Kexue Jishu Chubanshe. 169pp.

APPENDICES

CHAPTER

TWO

Table A2.1.1(n) Leaf form variables (outer leaves) means ± S.E. for different *Actinidia* taxa

Taxon	Lamina area (cm^2)	Lamina length (cm)	Lamina width (cm)	Petiole length (cm)	Specific area ($cm^2.g^{-1}$)
A. arguta var. *arguta*	114.38 ± 7.77	15.53 ± 0.47	10.41 ± 0.37	8.79 ± 0.76	145.19 ± 5.61
A. arguta var. *cordifolia*	44.71 ± 2.35	8.76 ± 0.19	6.87 ± 0.18	5.96 ± 0.47	124.44 ± 5.15
A. rufa	115.28 ± 5.97	14.37 ± 0.43	10.61 ± 0.21	5.74 ± 0.14	101.80 ± 2.89
A. melanandra var. *melanandra*	31.20 ± 1.72	11.36 ± 0.23	4.31 ± 0.13	5.02 ± 0.17	107.64 ± 13.61
A. kolomikta	59.36 ± 2.42	11.17 ± 0.31	7.80 ± 0.20	3.50 ± 0.22	143.66 ± 4.47
A. polygama	141.26 ± 3.01	16.22 ± 0.21	12.98 ± 0.17	5.62 ± 0.21	128.84 ± 3.46
A. valvata	83.34 ± 4.36	13.78 ± 0.37	9.04 ± 0.32	6.18 ± 0.40	109.09 ± 6.15
A. callosa var. *henryi*	49.42 ± 2.15	9.79 ± 0.27	6.79 ± 0.15	2.74 ± 0.07	127.16 ± 5.32
A. chrysantha	68.53 ± 4.25	15.61 ± 1.56	7.34 ± 0.25	4.06 ± 0.20	86.37 ± 4.35
A. indochinensis	44.86 ± 2.34	12.25 ± 0.22	5.66 ± 0.18	3.59 ± 0.09	81.99 ± 1.14
A. melliana	107.38 ± 5.28	26.57 ± 0.92	6.41 ± 0.18	3.28 ± 0.12	82.92 ± 4.65
A. hemsleyana var. *hemsleyana*	113.27 ± 3.15	22.05 ± 0.66	8.03 ± 0.17	3.66 ± 0.14	115.45 ± 5.00
A. latifolia	156.75 ± 6.35	17.33 ± 0.23	12.65 ± 0.27	6.40 ± 0.22	116.25 ± 5.02
A. eriantha	189.52 ± 8.98	21.90 ± 0.38	12.66 ± 0.41	9.24 ± 0.33	148.20 ± 6.66
A. chinensis var. *chinensis* 3/6/14b*	215.63 ± 7.30	13.61 ± 0.29	16.95 ± 0.41	15.30 ± 0.55	133.86 ± 9.55
A. chinensis var. *chinensis* 460.4*	196.76 ± 10.93	11.93 ± 0.29	14.05 ± 0.37	9.63 ± 0.36	113.19 ± 3.63
A. chinensis var. *chinensis* 460.9*	131.84 ± 3.79	12.15 ± 0.29	13.52 ± 0.29	10.23 ± 0.36	116.34 ± 3.70
A.deliciosa var. *deliciosa* 'Hayward'	223.54 ± 8.68	12.76 ± 0.27	18.40 ± 0.40	6.95 ± 0.29	69.77 ± 1.51
A.deliciosa var. *deliciosa* 'Matua'	167.05 ± 5.94	12.45 ± 0.22	14.68 ± 0.33	7.40 ± 0.52	117.49 ± 3.20
A. deliciosa var. *deliciosa* 'Bruno'	194.15 ± 11.46	13.74 ± 0.26	15.70 ± 0.55	8.44 ± 0.30	80.56 2.63
A. deliciosa var. *chlorocarpa*	187.81 ± 7.09	14.41 ± 0.33	15.68 ± 0.38	9.75 ± 0.45	97.68 ± 2.42

Footnote : * Numbers are different genotypes

Table A2.1.1 Cont

Table A2.1.1(b) Leaf form variables (outer leaves) means ± S.E. for different *Actinidia* taxa

Taxon	Length : width ($cm.cm^{-1}$)	H_2O wt (g)	Specific wt ($g.cm^{-2}$) ($mg.cm^{-2}$)	leaf dry wt (g)	Leaf wet wt (g)	leaf dry wt % of fresh wt.
A. arguta var. *arguta*	1.50 ± 0.03	2.41 ± 0.18	0.0068 6.88	0.82 ± 0.08	3.23 ± 0.26	24.78 ± 0.50
A. arguta var. *cordifolia*	1.28 ± 0.02	0.84 ± 0.05	0.0080 8.03	0.37 ± 0.03	1.22 ± 0.08	30.53 ± 1.09
A. rufa	1.36 ± 0.04	2.48 ± 0.13	0.0098 9.82	1.13 ± 0.05	3.62 ± 0.17	31.50 ± 0.39
A. melanandra var. *melanandra*	2.67 ± 0.08	0.64 ± 0.04	0.0093 9.30	0.31 ± 0.02	0.97 ± 0.06	33.19 ± 0.46
A. kolomikta	1.43 ± 0.04	0.84 ± 0.04	0.0069 6.96	0.42 ± 0.02	1.27 ± 0.06	32.27 ± 0.76
A. polygama	1.25 ± 0.02	2.40 ± 0.06	0.0076 7.76	1.11 ± 0.04	3.46 ± 0.12	31.58 ± 0.46
A. valvata	1.54 ± 0.04	2.04 ± 0.12	0.0091 9.16	0.79 ± 0.04	2.83 ± 0.16	27.30 ± 0.61
A. callosa var. *henryi*	1.44 ± 0.03	1.07 ± 0.05	0.0078 7.86	0.40 ± 0.02	1.48 ± 0.07	26.96 ± 0.54
A. chrysantha	1.86 ± 0.07	1.43 ± 0.07	0.0115 11.57	0.80 ± 0.04	2.24 ± 0.11	35.74 ± 0.50
A. indochinensis	2.19 ± 0.06	0.88 ± 0.05	0.0122 12.19	0.54 ± 0.02	1.43 ± 0.07	38.31 ± 0.26
A. melliana	4.14 ± 0.09	3.14 ± 0.18	0.0120 12.05	1.36 ± 0.08	4.51 ± 0.25	30.27 ± 0.59
A. hemsleyana var. *hemsleyana*	2.76 ± 0.10	2.38 ± 0.15	0.0086 8.60	1.02 ± 0.05	3.67 ± 0.16	27.69 ± 0.88
A. latifolia	1.37 ± 0.02	3.67 ± 0.20	0.0086 8.60	1.36 ± 0.08	5.04 ± 0.28	27.05 ± 0.38
A. eriantha	1.75 ± 0.04	3.77 ± 0.22	0.0067 6.74	1.35 ± 0.07	5.16 ± 0.31	26.40 ± 0.61
A. chinensis var. *chinensis* 3/6/14b*	0.80 ± 0.02	5.28 ± 0.22	0.0074 7.47	1.83 ± 0.08	7.11 ± 0.30	25.66 ± 0.32
A. chinensis var. *chinensis* 460.4*	0.86 ± 0.02	9.00 ± 0.27	0.0088 8.83	1.27 ± 0.08	4.07 ± 0.23	31.38 ± 0.48
A. chinensis var. *chinensis* 460.9*	0.90 ± 0.03	3.03 ± 0.09	0.0086 8.59	1.15 ± 0.04	4.19 ± 0.13	27.51 ± 0.44
A.deliciosa var. *deliciosa* 'Hayward'	0.69 ± 0.01	6.44 ± 0.33	0.0143 14.33	3.23 ± 0.15	9.81 ± 0.47	33.11 ± 0.78
A.deliciosa var. *deliciosa* 'Matua'	0.85 ± 0.02	4.01 ± 0.15	0.0085 8.51	1.44 ± 0.06	5.40 ± 0.21	26.70 ± 0.54
A. deliciosa var. *deliciosa* 'Bruno'	0.88 ± 0.02	6.22 ± 0.47	0.0124 12.41	0.95 ± 0.05	3.79 ± 0.24	28.69 ± 0.28
A. deliciosa var. *chlorocarpa*	0.92 ± 0.02	4.68 ± 0.27	0.010 10.23	1.95 ± 0.10	6.63 ± 0.35	29.75 ± 1.10

Footnote : * Numbers are different genotypes

Table A2.1.2(a) Leaf form variables (inner leaves) means ± S.E. for different *Actinidia* taxa

Taxon	Lamina area (cm^2)	Lamina length (cm)	Lamina width (cm)	Petiole length (cm)	Specific are (cm^2g^{-1})
A. arguta var. *arguta*	88.77 ± 4.58	13.09 ± 0.57	9.35 ± 0.23	10.34 ± 0.54	231.12 ± 15.90
A. arguta var. *cordifolia*	41.96 ± 2.13	8.05 ± 0.36	6.61 ± 0.16	6.39 ± 0.32	202.86 ± 12.63
A. rufa	70.71 ± 0.04	11.93 ± 0.92	9.06 ± 0.71	9.46 ± 0.51	183.44 ± 13.32
A. melanandra var. *melanandra*	24.22 ± 1.55	10.16 ± 0.30	3.72 ± 0.15	5.24 ± 0.18	114.95 ± 2.43
A. kolomikta	44.37 ± 3.26	8.73 ± 0.48	6.72 ± 0.23	4.51 ± 0.32	228.51 ± 16.76
A. polygama	45.31 ± 5.02	11.51 ± 0.48	8.15 ± 0.32	3.87 ± 0.27	210.12 ± 12.53
A. valvata	45.71 ± 3.17	10.60 ± 0.43	6.34 ± 0.25	6.39 ± 0.48	171.19 ± 4.69
A. callosa var. *henryi*	33.02 ± 1.69	8.73 ± 0.24	5.50 ± 0.15	5.98 ± 0.35	218.12 ± 11.44
A. chrysantha	40.36 ± 2.58	12.41 ± 0.57	4.98 ± 0.15	4.22 ± 0.17	107.51 ± 6.32
A. indochinensis	22.34 ± 1.68	8.96 ± 0.38	3.83 ± 0.15	2.64 ± 0.15	133.54 ± 5.42
A. melliana	63.45 ± 4.63	19.02 ± 0.95	4.74 ± 0.19	3.98 ± 0.26	102.66 ± 6.12
A. hemsleyana var. *hemsleyana*	70.75 ± 5.67	16.73 ± 0.76	5.98 ± 0.23	5.84 ± 0.34	176.60 ± 9.02
A. latifolia	87.92 ± 5.70	13.22 ± 0.48	9.02 ± 0.41	6.69 ± 0.19	170.50 ± 8.69
A. eriantha	103.10 ± 6.75	16.12 ± 0.48	9.09 ± 0.39	4.05 ± 0.16	222.58 ± 17.69
A. chinensis var. *chinensis* 3/6/14b*	113.62 ± 6.50	12.18 ± 0.31	11.57 ± 0.47	12.21 ± 0.34	121.81 ± 5.52
A. chinensis var. *chinensis* 460.4*	83.20 ± 4.56	9.42 ± 0.22	10.62 ± 0.37	9.38 ± 0.47	162.55 ± 10.26
A. chinensis var. *chinensis* 460.9*	108.90 ± 5.45	10.71 ± 0.46	11.98 ± 0.42	14.04 ± 0.62	171.94 ± 10.93
A. deliciosa var. *deliciosa* 'Hayward'	139.82 ± 9.37	10.55 ± 0.40	14.12 ± 0.50	10.12 ± 0.50	101.16 ± 3.85
A. deliciosa var. *deliciosa* 'Matua'	-	-	-	-	-
A. deliciosa var. *deliciosa* 'Bruno'	125.72 ± 8.57	11.44 ± 0.38	11.84 ± 0.46	9.81 ± 0.53	133.04 ± 7.06
A. deliciosa var. *chlorocarpa*	147.65 ± 11.28	13.22 ± 0.54	13.32 ± 0.56	13.74 ± 0.70	171.75 ± 6.68

Table A2.1.2 (

Footnote : * Numbers are different genotypes

Table A2.1.2(b) Leaf form variables (inner leaves) means ± S.E. for different *Actinidia* taxa

Taxon	Length : width ($cm.cm^{-1}$)	H_2O wt (g)	Specific wt ($g.cm^{-2}$) ($mg.cm^{-2}$)	leaf dry wt (g)	Leaf wet wt (g)	leaf dry wt % of fresh wt.
A. arguta var. *arguta*	1.39 ± 0.05	1.60 ± 0.09	0.0043 4.32	0.40 ± 0.02	2.01 ± 0.12	20.00 ± 0.48
A. arguta var. *cordifolia*	1.28 ± 0.07	0.67 ± 0.04	0.0049 4.92	0.22 ± 0.02	0.87 ± 0.07	26.36 ± 1.54
A. rufa	1.31 ± 0.005	1.13 ± 0.10	0.0054 5.45	0.41 ± 0.31	1.54 ± 0.31	27.12 ± 0.96
A. melanandra var. *melanandra*	2.75 ± 0.06	0.46 ± 0.03	0.0086 8.69	0.21 ± 0.01	4.51 ± 0.25	31.17 ± 0.34
A. kolomikta	1.29 ± 0.05	0.53 ± 0.06	0.0043 4.37	0.21 ± 0.02	0.71 ± 0.08	29.77 ± 0.99
A. polygama	1.44 ± 0.06	0.95 ± 0.07	0.0047 4.76	0.31 ± 0.02	1.27 ± 0.09	24.73 ± 0.85
A. valvata	1.67 ± 0.03	0.89 ± 0.07	0.0058 5.84	0.27 ± 0.02	0.17 ± 0.09	23.46 ± 0.54
A. callosa var. *henryi*	1.59 ± 0.04	0.46 ± 0.02	0.0045 4.58	0.16 ± 0.01	0.62 ± 0.03	25.28 ± 0.54
A. chrysantha	2.49 ± 0.10	0.90 ± 0.10	0.0093 9.30	0.39 ± 0.03	1.15 ± 0.08	33.98 ± 1.12
A. indochinensis	2.34 ± 0.08	0.31 ± 0.03	0.0074 7.48	0.17 ± 0.01	0.49 ± 0.04	35.44 ± 0.55
A. melliana	4.03 ± 0.17	1.50 ± 0.13	0.0097 9.74	0.63 ± 0.05	2.09 ± 0.18	29.98 ± 0.36
A. hemsleyana var. *hemsleyana*	2.78 ± 0.05	1.63 ± 0.16	0.0056 5.66	0.43 ± 0.04	2.06 ± 0.20	20.80 ± 0.78
A. latifolia	1.48 ± 0.05	1.83 ± 0.19	0.0058 5.86	0.54 ± 0.05	2.37 ± 0.24	23.19 ± 1.32
A. eriantha	1.81 ± 0.05	2.12 ± 0.15	0.0044 4.49	0.50 ± 0.04	2.62 ± 0.18	18.84 ± 0.55
A. chinensis var. *chinensis* 3/6/14b*	1.01 ± 0.05	2.60 ± 0.16	0.0082 8.21	0.94 ± 0.06	3.54 ± 0.21	26.70 ± 0.78
A. chinensis var. *chinensis* 460.4*	0.91 ± 0.03	1.45 ± 0.10	0.0061 6.15	0.56 ± 0.06	2.02 ± 0.17	27.69 ± 0.74
A. chinensis var. *chinensis* 460.9*	0.93 ± 0.57	1.98 ± 0.14	0.0058 5.81	0.69 ± 0.06	2.68 ± 0.20	25.63 ± 0.59
A. deliciosa var. *deliciosa* 'Hayward'	0.74 ± 0.01	3.11 ± 0.20	0.0098 9.88	1.39 ± 0.10	4.49 ± 0.28	30.80 ± 0.82
A. deliciosa var. *deliciosa* 'Matua'	-	-	-	-	-	-
A. deliciosa var. *deliciosa* 'Bruno'	0.97 ± 0.03	5.24 ± 0.51	0.0075 7.51	0.95 ± 0.05	3.79 ± 0.24	25.41 ± 2.12
A. deliciosa var. *chlorocarpa*	1.04 ± 0.02	3.03 ± 0.27	0.0058 5.82	0.90 ± 0.08	3.93 ± 0.37	22.94 ± 0.36

Footnote : * Numbers are different genotypes

Table A2.1.3

n = 20 outer leaves; n = 20 inner leaves per taxon
Ranges of leaf size variables
(*) Lamina length of condate base in (+) cm (Condon 1991)

Taxon	Lamina area (cm^2)	Lamina length (cm)	Lamina width (cm)	Petiole length (cm)
A. arguta var. *arguta*	62.63 - 177.69	9.0 - 20.7	7.2 - 14.0	4.5 - 15.0
A. arguta var.*cordifolia*	13.47 - 65.78	3.8 - 11.5	5.0 - 8.4	2.5 - 9.0
A. rufa	70.55 - 183.21	8.0 - 17.0 (+1.2)	4.5 - 12.5	3.5 - 12.7
A. melanandra var. *melanandra*	12.16 - 53.00	7.2 - 14.0	2.5 - 5.0	3.8 - 7.0
A. kolomikta	29.43 - 74.99	4.3 - (+0.5)13.0 (+0.5)	4.8 - 10.0	2.5 - 7.5
A. polygama	29.43 - 176.29	4.5 - (+0.5)13.0 (+0.5)	6.5 - 14.5	2.5 - 7.3
A. valvata	23.48 - 122.49	7.3 - 16.5	7.0 - 11.8	3.5 - 12.7
A. callosa var. *henryi*	24.16 - 62.18	6.7 - (+0.2)10.4 (+0.1)	4.0 - 8.3	2.3 - 10.2
A. chrysantha	22.09 - 102.91	7.2 - 17.20 (+0.20)	3.8 - 9.5	2.5 - 7.0
A. indochinensis	11.38 - 70.96	5.5 - 14.3	2.8 - 7.5	2.5 - 35.0
A. melliana	33.09 - 145.19	11.7 - 31.0	3.5 - 8.0	2.0 - 6.5
A. hemsleyana var. *hemsleyana*	30.80 - 132.89	11.2 - 33.0 (+0.2)	3.8 - 9.5	2.5 - 8.0
A. latifolia	45.31 - 214.43	8.2 - 19.0	6.5 - 15.2	4.5 - 9.0
A. eriantha	42.48 - 287.46	12.0 - 24.5	5.5 - 17.3	3.2 - 12.0
A. chinensis var. *chinensis* 3/6/14b*	69.72 - 253.61	8.5 - (+0.5)17.0 (+2.0)	6.5 - 19.3	8.5 - 20.0
A. chinensis var. *chinensis* 460.4*	52.21 - 191.58	7.5 - (+1.2)14.0 (+3.5)	7.9 - 16.5	6.8 - 14.5
A. chinensis var. *chinensis* 460.9*	63.63 - 162.71	8.8 - 14.5 (+2.0)	7.0 - 15.2	7.3 - 14.5
A. deliciosa var. *deliciosa* cv.'Hayward'	94.43 - 307.93	8.5 - (+1.5)15.5 (+4.0)	11.5- 22.0	6.0 - 15.0
A. deliciosa var. *deliciosa* cv.'Matua'	119.54 - 215.75	11.3 - (+2.0)16.5 (+3.5)	11.4- 17.2	5.3 - 10.0
A. deliciosa var. *deliciosa* cv.'Bruno'	81.12 - 273.64	8.0 - (+0.2)16.5 (+3.5)	10.0- 20.0	6.2 - 14.5
A. deliciosa var. *chlorocarpa*	80.67 - 241.93	9.5 - (+1.0)18.7	9.8 - 19.0	6.2 - 18.5

Footnotes : + = outer leaves only
* = Numbers are different genotypes

Table A2.1.4

Ranges of leaf size variables derived from Chinese *Actinidia* (Liang 1984)

Taxon	Lamina area (cm^2)	Lamina length (cm)	Lamina width (cm)	Petiole length (cm)
A. arguta var. *arguta*	N. A.	6 - 9	4.5 - 8	3-6* (- 10)
A. arguta var.*cordifolia*	N. A.	5 - 10	4 - 8	3 - 6* (- 10)
A. rufa	N. A.	N. A.	N. A.	N. A.
A. melanandra var. *melanandra*	N. A.	7 - 11	3.5 - 4.5	1.5 - 5.5*
*A. kolomikta**	N. A.	6 - 15	5 - 10	2.5 - 5*
A. polygama	N. A.	7 - 14	4.5 - 8	1.5 - 3.5*
A. valvata	N. A.	5 - 13	2.5 - 7.5	N. A.
A. callosa var. *henryi*	N. A.	8 - 10	4 - 5.5	2 - 8*
A. chrysantha	N. A.	7 - 14	4.5 - 6.5	2.5 - 5
A. indochinensis	N. A.	4 - 10	3.5 - 5	2 - 3
A. melliana	N. A.	N. A.	N. A.	N. A.
A. hemsleyana	N. A.	8,12,17 22	3,4.5,5 8.5	10 - 18
A. latifolia	N. A.	8 - 13 occ. 15	5 - 8.5 occ. 12	3 - 7
A. eriantha	N. A.	8 - 16	6 - 11	1.5 - 3
A. chinensis var. *chinensis*	N. A.	6 - 8	7 - 8	N. A.
A. chinensis var. *hispida*	N. A.	9 - 10	8 - 10	N. A.

Footnotes :

1. * = taken from general diagnosis (species) in Liang (1984)
2. N.A. = not available as data not specified by Liang (1984)
3. occ = occasionally
4. Condon (1991) in Tables A2.1.3-2.1.5 refers to the present thesis

Table A2.1.5

Leaf form measurements of some N.Z. cultivars of *Actinidia** (Adapted from Zhang and Thorp 1986)

Taxon	Lamina length (cm)	Lamina width (cm)	Petiole length (cm)	Petiole width (cm)
A. deliciosa cv. Hayward	14.22 ± 0.35	15.96 ± 0.34	10.64 ± 0.45	0.45 ± 0.01
A. deliciosa cv. Matua	11.44 ± 0.22	10.25 ± 0.19	5.34 ± 0.18	0.31 ± 0.07
A. deliciosa cv. Bruno	14.28 ± 0.27	14.04 ± 0.35	9.03 ± 0.45	0.43 ± 0.01

* Also obtained from the N.Z., D.S.I.R. Kiwifruit germplasm collection

APPENDIX 2.2.1

Summer shoot characters used in cluster analysis

Character	Type	Description	Character States
1	Type = 2	2 yr cane colour	1 = green +/- brown 2 = brown or chestnut brown 3 = brown + red or purple
2	Type = 3	1 yr cane glaucous	0 = absent 1 = present
3	Type = 2	2 yr cane texture	1 = smooth to polished 2 = smooth + warty (lenticels) 3 = rough asperous (hairs)
4	Type = 2	1 yr cane colour other than glaucous	1 = green or no other colour 2 = green brown 3 = green red 4 = brown + red or purple
5	Type = 2	1 yr cane lenticel profile	0 = low 1 = prominent
6	Type = 2	1 yr cane max. internode length	1 = medium 50-70 mm 2 = long 70-100 mm 3 = very long > 100 mm
7	Type = 2	leaf as a whole	0 = not arched but hanging 1 = arched
8	Type = 2	petiole course	0 = petioles not flicking and turning 1 = J-shaped petiole bases to reorient leaf blade
9	Type = 3	leaf apex re. plane of cane	0 = below plane of cane 1 = equal to or above
10	Type = 2	leaf flatness in the middle	0 = not planar, i.e. arched 1 = mainly planar
11	Type = 2	frequency of mature leaf shape types	Count of 1 or 2
	Type = 2	juvenile leaf shapes	1 = lanceolate only 2 = lanceolate and ovate 3 = ovate and/or widely ovate
13	Type = 2	juvenile shoot hair colour	1 = ginger absent 2 = ginger or brown 3 = ginger + white 4= red only

Character	Type	Description	Character States
14	Type = 1	Frequency of leaf base types	count of 1-5 inclusive
15	Type = 1	Lamina area (cm^2)	continuous variable
16	Type = 1	leaf length : width shape ratio	ratio variable
17	Type = 1	lamina width (cm)	continuous variable
18	Type = 1	petiole length (cm)	continuous variable
19	Type = 2	frequency of leaf apex types	count of 1 or 2
20	Type = 1	specific weight mg : cm^2 of leaf	ratio
21	Type = 1	wt of H_2O in g	continuous
22	Type = 2	type of venation	0 = semicraspedodromous 1 = craspedodromous (direct to margin)
23	Type = 1	1^0 vein thickness : lamina width	ratio
24	Type = 3	variations in divergence angle of 2^0 veins	0 = uniform angle 1 = basal veins > angle of upper
25	Type = 2	thickness of 2^0 vein c.f. 1^0 vein	0 = fine and hair-like 1 = moderate
26	Type = 2	areole perfection	0 = imperfectly dev. 1 = perfectly dev. or becoming so
27	Type = 2	max areole size	0 = max. size 0.3 - 1 mm, "medium" 1 = max. size $\geqslant$ 2 mm "large or v.large"
28	Type = 1	freq.margin types	count of 1-5 inclusive
29	Type = 2	margin orientation	1 = revolute 2 = slightly revolute 3 = planar
30	Type = 2	margin teeth orientation	0 = inward 45^0 re margin 1 = outward 90^0 re margin

Character	Type	Description	Character States
31	Type = 2	principal vein of tooth	0 = eccentric 1 = centric
32	Type = 2	adaxial leaf gloss	1 = matt 2 = semi-glossy 3 = glossy
33	Type = 2	adaxial leaf colour	1 = variegated + green 2 = entirely mid-green 3 = entirely dark green
34	Type = 2	distn. of adaxial surface hairs	0 = largely confined to veins 1 = mainly beyond veins
35	Type = 2	abaxial surface abundance of hairs	1 = glabrate or purberulous on veins only 2 = bearded in axils only 3 = bearded in axils plus hairs beyond veins
36	Type = 3	adaxial setose hairs	0 = absent 1 = present
37	Type = 1	frequency of palisade layers in cross-section	count 1, 2 or 3
38	Type = 1	palisade thickness : leaf thickness	ratio 0.20 0.50 0.75
39	Type = 1	1^0 vein : interveinal thickness ratio	ratio 3.8 → 15.5
40	Type = 2	lamina horizon relative to height of 1^0 vein bundle	0 = "level with" 1 = above
41	Type = 2	shape of 1^0 bundle near petiole base	0 = open or arc-shaped 1 = ring or closed
42	Type = 3	abundance of phenolics near 1^0 vein	0 = rare or absent 1 = common
43	Type = 3	types of ergastic Ca crystals	0 = raphides only 1 = raphides + "cubic" and/or styloids
44	Type = 2	spongy mesophyll cell shape	1 = globose 2 = globose to attenuate 3 = attenuated

Character	Type	Description	Character States
45	Type = 2	abaxial surface profile	1 = smooth 2 = slightly papillate 3 = papillate
46	Type = 3	stomatal protuberance	0 = not raised 1 = raised obviously so
47	Type = 3	adaxial bundle collenchyma	0 = absent 1 = present
48	Type = 1	max no. of sclerenchyma layers 1^0 bundle	count of 1-6 inclusive
49	Type = 3	interveinal hypoderm continuous	0 = absent 1 = present
50	Type = 3	epicuticular wax flakes	0 = absent 1 = present
51	Type = 3	pith solid or lamellate "chambered"	0 = chambered/lamellate 1 = completely solid
52	Type = 3	setose spiny hairs as 2^0 devt.	0 = absent 1 = present
53	Type = 3	simple abaxial hairs hispid	0 = absent 1 = present
54	Type = 3	simple abaxial hairs setose or hirsute	0 = absent 1 = present
55	Type = 3	abaxial bifids	0 = absent 1 = present
56	Type = 3	abaxial stellate hairs not obv. stalked	0 = absent 1 = present
57	Type = 3	abaxial stellate hairs stalked	0 = absent 1 = present

APPENDIX 2.2

Table A2.2.2 Table of Gower's Coefficients

	OTU no. ->	1	2	3	4	5	6
1	Argarg						
2	Argcord	0.7197					
3	Rufa	0.4757	0.5419				
4	Melan	0.4423	0.4938	0.4888			
5	Kolom	0.6170	0.6875	0.5985	0.4845		
6	Polyg3/12/11	0.6317	0.6521	0.5602	0.5140	0.7175	
7	Valv	0.6385	0.6491	0.5727	0.5298	0.6987	0.8147
8	Callhen	0.5048	0.5474	0.5957	0.5036	0.6574	0.5244
9	Chrys	0.4286	0.4501	0.6068	0.5250	0.5629	0.5121
10	Indoch36/3/11a	0.4501	0.4469	0.5228	0.4850	0.5143	0.4050
11	Mell	0.5493	0.4563	0.4480	0.4608	0.5218	0.5552
12	Hemsley	0.5752	0.5509	0.4633	0.5011	0.5342	0.5493
13	Latif	0.4529	0.4269	0.5293	0.2996	0.4254	0.3732
14	Erian	0.4493	0.4389	0.4730	0.2789	0.3985	0.3559
15	Chin3/6/14b	0.3380	0.4595	0.4960	0.2662	0.4035	0.3792
16	Chin460.4	0.3367	0.4576	0.5052	0.2718	0.4022	0.3779
17	Chin460.9	0.3558	0.4799	0.5230	0.2886	0.4214	0.3998
18	AdelBruno	0.3036	0.4440	0.4666	0.2650	0.3083	0.3040
19	AdelHay	0.2807	0.4389	0.5016	0.2601	0.3431	0.3202
20	AdelMatua	0.3054	0.4236	0.4976	0.2792	0.3475	0.3228
21	AdelChlorocarpa	0.3320	0.4958	0.4621	0.2490	0.3993	0.3948

	OTU no. ->	7	8	9	10	11	12
1	Argarg						
2	Argcord						
3	Rufa						
4	Melan						
5	Kolom						
6	Polyg3/12/11						
7	Valv						
8	Callhen	0.5961					
9	Chrys	0.6219	0.6002				
10	Indoch36/3/11a	0.5025	0.5819	0.8441			
11	Mell	0.5349	0.5036	0.6057	0.5941		
12	Hemsley	0.6015	0.5342	0.5678	0.4719	0.5326	
13	Latif	0.3895	0.4134	0.3292	0.3659	0.3084	0.4206
14	Erian	0.3498	0.3121	0.2449	0.2613	0.3017	0.3729
15	Chin3/6/14b	0.3336	0.3814	0.3365	0.3129	0.2250	0.4549
16	Chin460.4	0.3331	0.3822	0.3423	0.3187	0.2340	0.4643
17	Chin460.9	0.3560	0.4013	0.3598	0.3362	0.2510	0.4830
18	AdelBruno	0.3009	0.3350	0.3133	0.3508	0.2226	0.4300
19	AdelHay	0.2757	0.3637	0.3481	0.3660	0.2574	0.3836
20	AdelMatua	0.2967	0.3750	0.3364	0.3366	0.2432	0.3968
21	AdelChlorocarpa	0.3639	0.3313	0.3032	0.2821	0.2660	0.4464

Table A2.2.2 continued

	OTU no. ->	13	14	15	16	17	18
1	Argarg						
2	Argcord						
3	Rufa						
4	Melan						
5	Kolom						
6	Polyg3/12/11						
7	Valv						
8	Callhen						
9	Chrys						
10	Indoch36/3/11a						
11	Mell						
12	Hemsley						
13	Latif						
14	Erian	0.7631					
15	Chin3/6/14b	0.6128	0.6865				
16	Chin460.4	0.6172	0.6895	0.9606			
17	Chin460.9	0.6328	0.6931	0.9606	0.9733		
18	AdelBruno	0.6141	0.6462	0.8650	0.8742	0.8619	
19	AdelHay	0.6116	0.6054	0.8571	0.8709	0.8567	0.9153
20	AdelMatua	0.6528	0.6512	0.8462	0.8622	0.8674	0.8859
21	AdelChlorocarpa	0.5626	0.6710	0.8501	0.8659	0.8631	0.8548

	OTU no. ->	19	20	21
1	Argarg			
2	Argcord			
3	Rufa			
4	Melan			
5	Kolom			
6	Polyg3/12/11			
7	Valv			
8	Callhen			
9	Chrys			
10	Indoch36/3/11a			
11	Mell			
12	Hemsley			
13	Latif			
14	Erian			
15	Chin3/6/14b			
16	Chin460.4			
17	Chin460.9			
18	AdelBruno			
19	AdelHay			
20	AdelMatua	0.9037		
21	AdelChlorocarpa	0.8162	0.8213	

Herbarium specimens from East Asia examined at
Botany Division, D.S.I.R., Lincoln (Dec. 19, 1990).

Table A2.3 : List of Herbarium specimens consulted

Section/Taxon	Herbarium voucher code	Location	Detd. by
Leiocarpae:			
A. arguta	CHR 381774A	wild, Jap.	Y.T.
	CHR 380053	wild, Honshu, Jap.	Y.T.
A. kolomikta	CHR 445031	wild, Honshu, Jap.	M.I.T.
Maculatae:			
A. rubricaulis var. *coriacea*	CHR 411289	cvd, G.I.B.	C.F.L.
A. chrysantha (M)	CHR 411283	cvd, G.I.B.	C.F.L.
A. cylindrica var. *reticulata*	CHR 422183	cvd, G.I.B.	C.F.L.
A. glaucophylla	CHR 411000	wild, Guangdong, Ch.	K.S.
A. indochinensis (M)	CHR 411296	cvd, G.I.B.	C.F.L.
..... (F)	CHR 411295	wild, Guangxi, Ch.	C.F.L.
Stellatae (Perfectae)			
A. styracifolia	CHR 422177	cvd, G.I.B.	C.F.L.
A. eriantha (F)	CHR 411288	cvd, G.I.B.	C.F.L.
(M)	CHR 411287	cvd, G.I.B.	C.F.L.
A. chinensis	CHR 446225	wild, Anhui, Ch.	K.Y.
A. deliciosa	CHR 446246	wild, Guizhou, Ch.	N.A.
A. deliciosa var. *chlorocarpa*	CHR 411285	cvd, G.I.B.	C.F.L.
	CHR 411244	cvd, G.I.B.	C.F.L.

Key : cvd = cultivated, G.I.B. = Guangxi Institute of Botany (research orchard),
Jap. = Japan, Ch. = China; CHR = Bot. Div. herbarium code (international)
detd = determined by:
Y.T. = Y. Tateishi, M.I.T. = Murata, Im and Chang
C.F.L. = C.F. Liang, K.Y. = K. Yao; K.S. = K.L. Shi
N.A. = not available part of expedition
Sex of plant : (M) = male; (F) = female

APPENDICES

CHAPTER THREE

APPENDIX 3.1

LIST OF WINTER SHOOT CHARACTERS USED IN CLUSTER ANALYSIS

Continuous, ordered multistate characters (units in brackets)

Arithmetic means

Character

1 Bud-case length (1 mm)
2 Bud-case height (mm)
3 Bud-case width (mm)
4 Ostiole width (mm)
5 Cane diameter (mm)
6 Height of visible bud structures protruding, above the ostiole surface (mm)
7 Number of bud structures externally visible through the ostiole
8 Length of petiole diameter (mm)
9 Ostiole length (mm)
10 Base of bud-case to highest vertical point (mm)
11 Depth of petiole scar (mm)
12 Lenticel frequency on one side of bud-case
13 Lenticel density (count. cm^{-2})
14 Longest lenticel near bud (mm)
15 Cane hair base density (count. cm^{-2})

Ratios

16 Bud-case length/bud-case height
17 Bud-case width/ostiole width
18 Bud-case height/cane diameter
19 Number of visible structures/ostiole width

Continued...

Ratios

Character

20 B.T.O.H./bud-case length

21 Depth of petiole scar/bud-case height

Discrete, non-ordered characters

22 Stem colour

(Character states)

1 = chestnut-brown

2 = dark or chocolate brown

3 = fawn-brown

4 = green-ochre

5 = green-white

Dichotomous, two-state characters

23 Number of shoots per bud-case

(Character states)

1.00

or

3.00

APPENDIX 3.2

Table A3.2 **Table of Gower's coefficients**

	OTU no. ->	1	2	3	4	5	6
1	ARGARG						
2	ARGCORD	0.7934					
3	ARGGIR	0.8544	0.8290				
4	ARGPURP	0.8434	0.7910	0.8490			
5	RUFA	0.6440	0.6494	0.6808	0.7345		
6	MELAN	0.7769	0.7929	0.8165	0.8092	0.7023	
7	KOLOM	0.8015	0.6801	0.7662	0.7813	0.6577	0.7982
8	POLYG3/12/11	0.6943	0.6690	0.7316	0.7514	0.7629	0.7688
9	POLYG3/12/9A	0.7162	0.7579	0.7517	0.7841	0.7781	0.7697
10	VALV	0.7223	0.7007	0.7661	0.7898	0.7445	0.7660
11	CALLHEN	0.6042	0.5344	0.6038	0.6453	0.6479	0.6827
12	CHRYS	0.6996	0.6604	0.7377	0.7503	0.8045	0.7903
13	INDOCH36/3/11A	0.6461	0.5810	0.7015	0.6888	0.7364	0.6973
14	INDOCH36/3/8B	0.6297	0.5374	0.6492	0.6524	0.6893	0.6444
15	MELL	0.6020	0.5884	0.6305	0.6661	0.7552	0.7101
16	HEMSLEY	0.6669	0.6810	0.7074	0.7339	0.8491	0.7455
17	ERIAN	0.4930	0.5308	0.5211	0.5732	0.7031	0.5932
18	LATIF	0.5118	0.5139	0.5177	0.5639	0.7305	0.5802
19	ADELHAY	0.5165	0.5461	0.5518	0.6024	0.6788	0.5997
20	ADELBRUNO	0.5833	0.6036	0.6264	0.6625	0.6867	0.6726
21	ADELABBOTT	0.5712	0.5883	0.5974	0.6505	0.6818	0.6558
22	ADELGRACIE	0.5648	0.5814	0.6098	0.6508	0.6605	0.6222
23	ADELGREENSILL	0.5555	0.6281	0.5861	0.6367	0.6650	0.6180
24	ADELALLISON	0.6278	0.6336	0.6476	0.6977	0.7097	0.6906
25	ADELMATUA	0.6414	0.6359	0.6798	0.7316	0.7603	0.7005
26	ADELJONES	0.5594	0.6136	0.5964	0.6351	0.7160	0.6147
27	ADELMONTY	0.5841	0.6321	0.6593	0.6594	0.7103	0.6455
28	ADELELMWOOD	0.4614	0.5061	0.5408	0.5579	0.6921	0.5507
29	ADELCHLOROCARPA	0.6587	0.6765	0.6946	0.7272	0.7188	0.7601
30	ACHIN460/4	0.5310	0.5391	0.5745	0.6701	0.7840	0.6185
31	ACHIN460/9	0.4652	0.4452	0.5058	0.5486	0.6705	0.5576
32	ACHIN32	0.4907	0.4953	0.5304	0.5764	0.6898	0.5821

	OTU no. ->	7	8	9	10	11	12
1	ARGARG						
2	ARGCORD						
3	ARGGIR						
4	ARGPURP						
5	RUFA						
6	MELAN						
7	KOLOM						
8	POLYG3/12/11	0.7167					
9	POLYG3/12/9A	0.7045	0.8679				
10	VALV	0.7197	0.8594	0.8783			
11	CALLHEN	0.6670	0.5912	0.5846	0.6127		
12	CHRYS	0.7671	0.7650	0.7512	0.7799	0.7630	
13	INDOCH36/3/11A	0.6680	0.7286	0.7479	0.7710	0.6311	0.7516
14	INDOCH36/3/8B	0.6961	0.6967	0.6837	0.7060	0.6718	0.7338
15	MELL	0.6730	0.6710	0.6944	0.6738	0.6780	0.7897
16	HEMSLEY	0.6785	0.7403	0.7793	0.7687	0.6623	0.8075
17	ERIAN	0.5585	0.5861	0.6305	0.6158	0.6123	0.6827
18	LATIF	0.5608	0.6499	0.6613	0.6434	0.5958	0.6985
19	ADELHAY	0.5728	0.6492	0.6718	0.6715	0.5068	0.6649
20	ADELBRUNO	0.6441	0.6776	0.6982	0.6996	0.5099	0.6756
21	ADELABBOTT	0.6249	0.6741	0.7293	0.7027	0.5150	0.6649
22	ADELGRACIE	0.5867	0.6717	0.7037	0.7054	0.4728	0.6427
23	ADELGREENSILL	0.5646	0.6534	0.7050	0.6794	0.4503	0.6186
24	ADELALLISON	0.6656	0.7302	0.7575	0.7481	0.5725	0.7200
25	ADELMATUA	0.6692	0.7552	0.7746	0.7780	0.5821	0.7534
26	ADELJONES	0.5590	0.6540	0.7024	0.6897	0.4587	0.6255
27	ADELMONTY	0.5963	0.6713	0.7151	0.7091	0.5194	0.6712
28	ADELELMWOOD	0.5151	0.5972	0.6361	0.6142	0.5133	0.6442
29	ADELCHLOROCARPA	0.7095	0.7298	0.7670	0.7500	0.6197	0.7418
30	ACHIN460/4	0.5848	0.6919	0.7072	0.6890	0.6486	0.7455
31	ACHIN460/9	0.5338	0.6375	0.6127	0.6342	0.6592	0.6949
32	ACHIN32	0.5428	0.6157	0.6222	0.6467	0.6234	0.7029

	OTU no. ->	13	14	15	16	17	18
1	ARGARG						
2	ARGCORD						
3	ARGGIR						
4	ARGPURP						
5	RUFA						
6	MELAN						
7	KOLOM						
8	POLYG3/12/11						
9	POLYG3/12/9A						
10	VALV						
11	CALLHEN						
12	CHRYS						
13	INDOCH36/3/11A						
14	INDOCH36/3/8B	0.8367					
15	MELL	0.6329	0.6033				
16	HEMSLEY	0.7352	0.6658	0.7724			
17	ERIAN	0.5796	0.5414	0.6923	0.7477		
18	LATIF	0.6759	0.6468	0.6998	0.7013	0.7235	
19	ADELHAY	0.5804	0.5232	0.6760	0.6959	0.6911	0.6482
20	ADELBRUNO	0.5677	0.5207	0.6645	0.7463	0.7094	0.6433
21	ADELABBOTT	0.5959	0.5387	0.7013	0.7346	0.6811	0.6405
22	ADELGRACIE	0.5865	0.5239	0.6518	0.6971	0.6066	0.6247
23	ADELGREENSILL	0.5616	0.4995	0.6613	0.6947	0.6163	0.6381
24	ADELALLISON	0.6406	0.6012	0.7198	0.7422	0.6844	0.6493
25	ADELMATUA	0.6718	0.6379	0.7374	0.7637	0.6807	0.6871
26	ADELJONES	0.5952	0.5079	0.6413	0.7164	0.6030	0.6466
27	ADELMONTY	0.6059	0.5700	0.6584	0.7515	0.6549	0.6509
28	ADELELMWOOD	0.5695	0.5274	0.6762	0.6916	0.6878	0.6901
29	ADELCHLOROCARPA	0.6310	0.5943	0.7422	0.7378	0.7144	0.6844
30	ACHIN460/4	0.7355	0.6978	0.7377	0.7757	0.7644	0.8455
31	ACHIN460/9	0.6775	0.6842	0.6373	0.6353	0.6799	0.8099
32	ACHIN32	0.6640	0.6539	0.6954	0.7051	0.7159	0.8005

	OTU no. ->	19	20	21	22	23	24
1	ARGARG						
2	ARGCORD						
3	ARGGIR						
4	ARGPURP						
5	RUFA						
6	MELAN						
7	KOLOM						
8	POLYG3/12/11						
9	POLYG3/12/9A						
10	VALV						
11	CALLHEN						
12	CHRYS						
13	INDOCH36/3/11A						
14	INDOCH36/3/8B						
15	MELL						
16	HEMSLEY						
17	ERIAN						
18	LATIF						
19	ADELHAY						
20	ADELBRUNO	0.8115					
21	ADELABBOTT	0.8195	0.8252				
22	ADELGRACIE	0.8111	0.8387	0.8179			
23	ADELGREENSILL	0.8008	0.8182	0.7997	0.8664		
24	ADELALLISON	0.8164	0.8173	0.8418	0.8285	0.8118	
25	ADELMATUA	0.8146	0.8260	0.8292	0.8276	0.7930	0.8580
26	ADELJONES	0.7819	0.8026	0.8233	0.8672	0.8719	0.8071
27	ADELMONTY	0.8015	0.8260	0.8166	0.8391	0.8489	0.8169
28	ADELELMWOOD	0.8094	0.7845	0.7977	0.7848	0.7645	0.7456
29	ADELCHLOROCARPA	0.7829	0.8256	0.8213	0.7916	0.7730	0.8369
30	ACHIN460/4	0.7171	0.7034	0.6906	0.6921	0.6659	0.7205
31	ACHIN460/9	0.6183	0.5916	0.6050	0.5701	0.5314	0.6235
32	ACHIN32	0.6307	0.6450	0.6349	0.6287	0.6107	0.6701

APPENDIX 3.2

	OTU no. ->	25	26	27	28	29	30
1	ARGARG						
2	ARGCORD						
3	ARGGIR						
4	ARGPURP						
5	RUFA						
6	MELAN						
7	KOLOM						
8	POLYG3/12/11						
9	POLYG3/12/9A						
10	VALV						
11	CALLHEN						
12	CHRYS						
13	INDOCH36/3/11A						
14	INDOCH36/3/8B						
15	MELL						
16	HEMSLEY						
17	ERIAN						
18	LATIF						
19	ADELHAY						
20	ADELBRUNO						
21	ADELABBOTT						
22	ADELGRACIE						
23	ADELGREENSILL						
24	ADELALLISON						
25	ADELMATUA						
26	ADELJONES	0.7896					
27	ADELMONTY	0.8324	0.8469				
28	ADELELMWOOD	0.7427	0.7822	0.8321			
29	ADELCHLOROCARPA	0.8464	0.7742	0.8154	0.7381		
	ACHIN460/4	0.7769	0.6666	0.7007	0.7249	0.7261	
	ACHIN460/9	0.6448	0.5362	0.5906	0.6264	0.6530	0.7807
	ACHIN32	0.7192	0.5859	0.6439	0.6180	0.6723	0.8239

	OTU no. ->		32
1	ARGARG		
2	ARGCORD		
3	ARGGIR		
4	ARGPURP		
5	RUFA		
6	MELAN		
7	KOLOM		
8	POLYG3/12/11		
9	POLYG3/12/9A		
10	VALV		
11	CALLHEN		
12	CHRYS		
13	INDOCH36/3/11A		
14	INDOCH36/3/8B		
15	MELL		
16	HEMSLEY		
17	ERIAN		
18	LATIF		
19	ADELHAY		
20	ADELBRUNO		
21	ADELABBOTT		
22	ADELGRACIE		
23	ADELGREENSILL		
24	ADELALLISON		
25	ADELMATUA		
26	ADELJONES		
27	ADELMONTY		
28	ADELELMWOOD		
29	ADELCHLOROCARPA		
30	ACHIN460/4		
31	ACHIN460/9		
32	ACHIN32	0.7946	

Table A3.3

Data used in calculation of Gower similarity coefficients

SPECIES → / ↓ CHTRS (means)	arg.arg 1	arg.cord 2	arg.girald 3	arg.purp 4	rufa 5	melan. 6
1. Bud-case length (mm) (1)	9.90	12.30	11.40	11.20	11.50	8.15
2. Bud-case height (mm) (1)	3.40	4.10	3.60	3.85	5.37	4.25
3. Bud-case width (mm) (1)	5.60	6.55	5.00	6.10	5.87	6.25
4. Ostiole width (mm) (1)	0.25	0.23	0.44	0.62	3.04	1.50
5. Cane diameter (mm) (1)	8.22	10.97	8.45	7.18	9.85	8.64
6. Height visible bud structures (mm) (1)	0.00	0.12	0.28	0.39	1.80	0.25
7. Number of visible bud structures (count)(1)	1.00	0.10	0.60	1.00	4.50	0.30
8. L.P.D. petiole base (mm)(1)	3.35	3.35	3.35	4.24	4.17	3.10
9. Ostiole length (mm) (1)	0.23	0.19	0.23	0.17	2.32	0.34
10.Base to highest point (mm) (1)	4.30	4.58	4.20	4.80	6.30	3.70
11.Depth of petiole scar (mm) (1)	1.25	1.16	0.75	1.60	1.60	0.73
12.Lenticel freq. frequency side (count)(1)	3.80	6.60	2.20	3.90	3.70	1.90
13.Lenticel density (count.cm^{-2})(1)	47.40	32.00	29.60	40.40	9.00	33.80
14.Longest lenticel (mm) (1)	1.75	1.70	2.05	2.52	3.78	1.22
15.Cane hair base density (count.cm^{-2})(1)	0.00	0.00	0.00	0.00	910.00	0.00
16.Bud-case length/height (ratio)(2)	2.99	3.01	3.25	2.97	2.33	1.92
17.Bud-case width/ost. width (ratio)(2)	22.40	35.66	23.05	11.40	2.03	8.66
18.Bud-case height/cane diameter (ratio)(2)	0.42	0.38	0.43	0.55	0.55	0.50
19.Number visible structs/ost.width (ratio)(2)	4.00	0.22	1.90	1.90	1.47	0.46
20.BTOH/bud length (ratio)(2)	0.43	0.38	0.37	0.43	0.55	0.46
21.Depth of petiole scar/bud-height (ratio)(2)	0.37	0.28	0.21	0.41	0.32	0.17
22.Stem colour (2)	1.00	1.00	1.00	1.00	1.00	1.00
23.Number of shoots per bud (either 1 or 3) binary (2)	1.00	1.00	1.00	1.00	1.00	1.00

Table A3.3 continued....

Table A3.3 continued....

SPECIES → / ↓ CHTRS (means)	Kolom 7	Polyg. 3.12.11 8	Polyg. 3.12.9a 9	Valvata 10	Callosa II 11
1. Bud-case length (mm) (1)	7.10	8.00	11.25	10.50	6.41
2. Bud-case height (mm) (1)	3.85	3.85	4.25	3.80	5.02
3. Bud-case width (mm) (1)	3.92	6.15	5.70	6.93	5.73
4. Ostiole width (mm) (1)	0.50	1.40	1.55	1.75	5.36
5. Cane diameter (mm) (1)	5.53	8.45	8.39	7.56	7.10
6. Height visible bud structures (mm) (1)	0.27	0.50	0.35	0.60	2.75
7. Number of visible bud structures (count)(1)	1.10	2.10	1.40	2.75	9.10
8. L.P.D. petiole base (mm)(1)	1.95	3.75	3.84	3.41	2.91
9. Ostiole length (mm) (1)	0.47	0.97	0.97	0.83	3.18
10.Base to highest point (mm) (1)	3.65	4.20	6.05	5.42	3.21
11.Depth of petiole scar (mm) (1)	1.38	1.44	1.19	1.10	0.48
12.Lenticel freq. side (count)(1)	3.10	2.60	3.90	1.90	3.10
13.Lenticel density (count.cm^{-2})(1)	24.00	9.70	14.60	13.10	44.80
14.Longest lenticel (mm) (1)	0.90	4.89	3.25	2.31	1.47
15.Cane hair base density (count.cm^{-2})(1)	0.00	0.00	0.00	0.00	0.00
16.Bud-case length/height (ratio)(2)	1.88	2.26	2.70	2.84	1.30
17.Bud-case width/ost. width (ratio) (2)	10.44	4.66	3.70	4.10	1.08
18.Bud-case height/cane diameter (ratio)(2)	0.73	0.46	0.51	0.51	0.71
19.Number visible structs/ost.width (ratio)(2)	2.73	1.38	0.91	1.64	1.73
20.BTOH/bud length (ratio)(2)	0.51	0.52	0.54	0.52	0.51
21.Depth of petiole scar/bud-height (ratio)(2)	0.37	0.47	0.28	0.29	0.09
22.Stem colour (2)	1.00	3.00	3.00	3.00	1.00
23.Number of shoots per bud (either 1 or 3) binary(2)	1.00	1.00	1.00	1.00	3.00

Table A3.3 continued...

Table A3.3 continued....

SPECIES →	Chrys	Indoch 36.3.11a	Indoch 36.3.8b	Melliana	Hemsa
↓ CHTRS (means)	12	13	14	15	16
1. Bud-case length (mm) (1)	8.40	10.10	7.84	8.15	12.80
2. Bud-case height (mm) (1)	5.00	3.22	3.34	5.70	4.90
3. Bud-case width (mm) (1)	5.50	4.45	3.68	5.70	6.05
4. Ostiole width (mm) (1)	3.65	3.35	2.91	3.10	3.72
5. Cane diameter (mm) (1)	7.81	6.75	6.13	8.30	9.15
6. Height visible bud structures (mm) (1)	1.54	1.50	2.70	1.90	1.12
7. Number of visible bud structures (count)(1)	5.60	7.00	8.80	2.80	4.20
8. L.P.D. petiole base (mm) (1)	3.28	2.80	2.52	5.50	4.18
9. Ostiole length (mm) (1)	1.65	1.90	2.56	2.85	2.64
10. Base to highest point (mm) (1)	4.10	5.75	3.28	6.23	7.70
11. Depth of petiole scar (mm) (1)	1.47	0.50	0.47	4.00	1.29
12. Lenticel freq. side (count)(1)	1.90	2.30	2.60	2.50	2.50
13. Lenticel density (count.cm^{-2})(1)	15.40	10.00	12.90	21.60	9.60
14. Longest lenticel (mm) (1)	2.00	3.34	3.43	1.64	1.18
15. Cane hair base density (count.cm^{-2})(1)	0.00	0.00	0.00	102.70	265.00
16. Bud-case length/height (ratio)(2)	1.72	3.35	2.52	1.45	2.66
17. Bud-case width/ost. width (ratio)(2)	1.54	1.38	1.26	1.97	1.66
18. Bud-case height/cane diameter (ratio)(2)	0.66	0.48	0.55	0.69	0.53
19. Number of visible structs/ost. width (ratio)(2)	1.54	2.29	3.09	0.92	1.14
20. BTOH/bud length (ratio)(2)	0.48	0.57	0.42	0.77	0.60
21. Depth of petiole scar/bud height (ratio)(2)	0.30	0.17	0.15	0.70	0.27
22. Stem colour (2)	1.00	2.00	2.00	1.00	1.00
23. Number of shoots per bud (either 1 or 3) binary(2)	1.00	1.00	1.00	1.00	1.00

Table A3.3 continued...

Table A3.3 continued....

SPECIES → / ↓ CHTRS (means)	Erlantha 17	Latifolia 18	A. del. 'Hayward' 19	A. del. 'Bruno' 20	A. del 'Abbott' 21
1. Bud-case length (mm) (1)	12.20	11.45	14.10	16.10	16.00
2. Bud-case height (mm) (1)	6.90	6.80	7.50	8.00	7.00
3. Bud-case width (mm) (1)	7.10	7.00	7.65	7.70	7.00
4. Ostiole width (mm) (1)	5.55	6.45	2.30	1.22	1.77
5. Cane diameter (mm) (1)	8.35	10.75	8.55	9.60	8.20
6. Height visible bud structures (mm) (1)	2.22	3.45	0.70	0.38	0.37
7. Number of visible bud structures (count)(1)	5.50	6.20	3.00	1.10	1.50
8. L.P.D. petiole base (mm) (1)	4.70	5.10	6.78	6.30	5.80
9. Ostiole length (mm) (1)	4.05	4.80	2.12	1.25	1.92
10.Base to highest point (mm) (1)	7.00	6.45	9.62	8.10	10.50
11.Depth of petiole scar (mm) (1)	1.86	2.49	2.40	2.13	1.69
12.Lenticel freq. side (count)(1)	7.00	2.00	11.90	1.61	3.80
13.Lenticel density (count.cm^{-2})(1)	24.30	13.60	10.60	14.80	13.70
14.Longest lenticel (mm) (1)	1.32	4.20	2.02	1.53	0.76
15.Cane hair base density (count.cm^{-2})(1)	2027.00	0.00	80.80	500.00	98.80
16.Bud-case length/height (ratio)(2)	1.79	1.74	1.90	2.02	2.39
17.Bud-case width/ost. width (ratio)(2)	1.28	1.09	3.91	10.80	4.60
18.Bud-case height/cane diameter (ratio)(2)	0.83	0.63	0.90	0.83	0.90
19.Number of visible structs/ost.width (ratio)(2)	1.00	0.96	1.36	1.44	0.86
20.BTOH/bud-length (ratio)(2)	0.57	0.59	0.56	0.51	0.67
21.Depth of petiole scar/bud-height (ratio)(2)	0.27	0.37	0.31	0.27	0.24
22.Stem colour (2)	5.00	2.00	4.00	4.00	4.00
23.Number of shoots per bud (either 1 or 3) binary (2)	1.00	1.00	1.00	1.00	1.00

Table A3.3 continued...

Table A3.3 continued....

SPECIES → ↓ CHTRS (means)	A. del. 'Gracie' 22	A. del 'Greensill' 23	A. del. 'Allison' 24	A. del. 'Motun' 25	A. del 'Jones' 26
1. Bud-case length (mm) (1)	19.50	18.10	6.70	14.20	19.80
2. Bud-case height (mm) (1)	7.05	7.00	6.70	6.10	6.70
3. Bud-case width (mm) (1)	8.60	7.85	6.55	6.30	7.90
4. Ostiole width (mm) (1)	1.45	1.45	2.00	1.75	1.80
5. Cane diameter (mm) (1)	9.10	11.30	8.45	8.20	11.15
6. Height visible bud structures (mm) (1)	0.23	0.47	0.30	0.67	0.25
7. Number of visible bud structures (count)(1)	1.70	1.20	1.90	2.50	1.70
8. L.P.D. pet base (mm) (1)	7.10	6.80	5.70	5.40	6.90
9. Ostiole length (mm) (1)	1.50	1.35	1.70	1.70	1.60
10.Base to highest point (mm) (1)	9.86	9.15	9.01	6.42	11.68
11.Depth of petiole scar (mm) (1)	2.93	3.70	2.12	2.39	2.10
12.Lenticel freq. side (count)(1)	2.60	6.10	5.30	3.10	3.20
13.Lenticel density (count.cm^{-2})(1)	10.80	10.20	12.60	11.90	9.50
14.Longest lenticel (mm) (1)	2.22	1.80	1.61	2.25	1.73
15.Cane hair base density (count.cm^{-2})(1)	65.20	120.60	122.60	204.60	61.50
16.Bud-case length/height (ratio)(2)	2.83	2.68	2.78	2.41	3.06
17.Bud-case width/ost. width (ratio)(2)	6.40	6.60	4.43	4.64	4.70
18.Bud-case height/cane diameter. (ratio)(2)	0.77	0.63	0.80	0.75	0.62
19.Number of visible structs/ost.width (ratio)(2)	1.28	1.00	1.25	1.43	1.01
20.BTOH/bud-length (ratio)(2)	0.51	0.53	0.50	0.45	0.59
21.Depth of petiole scar/bud-height (ratio)(2)	0.42	0.54	0.33	0.40	0.32
22.Stem colour (2)	4.00	4.00	4.00	4.00	4.00
23.Number of shoots per bud (either 1 or 3) binary (2)	1.00	1.00	1.00	1.00	1.00

Table A3.3 continued...

Table A3.3 continued....

SPECIES → / ↓ CHTRS (means)	A. del. 'Monty' 27	A. del 'Elmwood' 28	A. del. 'Chlor[9]' 29	A. chin 460.4 30	A. chin 460.9 31	A. chin 32
1. Bud-case length (mm) (1)	18.00	17.50	11.52	12.50	9.30	12.10
2. Bud-case height (mm) (1)	7.35	9.00	6.57	6.35	6.95	5.80
3. Bud-case width (mm) (1)	7.80	8.80	7.07	6.30	7.15	6.65
4. Ostiole width (mm) (1)	2.20	3.30	1.40	5.00	6.50	6.30
5. Cane diameter (mm) (1)	10.60	10.20	8.90	8.98	7.90	7.80
6. Height visible bud structures (mm) (1)	0.70	2.00	0.28	2.37	3.57	4.30
7. Number of visible bud structures (count)(1)	2.20	3.70	1.50	6.70	10.20	7.60
8. L.P.D. pet base (mm) (1)	6.95	6.75	5.76	4.88	5.00	5.00
9. Ostiole length (mm) (1)	2.10	3.05	2.05	3.62	5.55	5.45
10. Base to highest point (mm) (1)	7.20	10.72	5.65	7.05	4.92	5.67
11. Depth of petiole scar (mm) (1)	1.40	1.89	1.20	2.51	0.87	3.41
12. Lenticel freq. side (count)(1)	4.00	4.70	3.20	2.90	2.80	1.70
13. Lenticel density (count.cm^{-2})(1)	10.50	16.60	26.70	10.90	8.30	8.10
14. Longest lenticel (mm) (1)	1.23	2.84	1.63	3.03	3.93	1.41
15. Cane hair base density (count.cm^{-2})(1)	223.60	107.20	146.40	301.00	8.20	391.00
16. Bud-case length/height (ratio)(2)	2.72	1.96	1.78	2.03	1.45	2.25
17. Bud-case width/ost. width (ratio)(2)	3.97	2.76	5.47	1.27	1.11	1.06
18. Bud-case height/cane diameter (ratio)(2)	0.71	0.89	0.74	0.71	1.00	0.78
19. Number of visible structs/ost.width (ratio)(2)	1.15	1.15	1.05	1.36	1.61	1.23
20. BTOH/bud-length (ratio)(2)	0.42	0.62	0.49	0.56	0.52	0.47
21. Depth of petiole scar/bud-height (ratio)(2)	0.21	0.21	0.18	0.41	0.12	0.65
22. Stem colour (2)	4.00	4.00	4.00	2.00	2.00	2.00
23. Number of shoots per bud (either 1 or 3) binary (2)	1.00	1.00	1.00	1.00	1.00	1.00

Footnotes :

(1) Characters are mostly arithmetic means of tabulated variables.
(1) = continuous variables
(2) = discrete non-ordered variables

(2) Character No.22 (1 yr. cane colour) is a ~~continuous~~ discrete non-ordered multi-state character.
Character states:
1 = chestnut brown,
2 = dark or chocolate brown
3 = fawn brown
4 = green ochre
5 = green white

APPENDICES

CHAPTER

FOUR

APPENDIX 4.1

Combined data set

winter and summer shoot characters

Table A4.1 TABLE OF GOWER'S COEFFICIENTS

	OTU no. ->	1	2	3	4	5	6
1	Argarg						
2	Argcord	0.7610					
3	Rufa	0.5558	0.6030				
4	Melan	0.4269	0.4483	0.4623			
5	Kolom	0.6978	0.7188	0.6430	0.4836		
6	Polyg3/12/11	0.6875	0.6917	0.6371	0.5191	0.7496	
7	Valv	0.6891	0.6927	0.6486	0.5213	0.7318	0.8601
8	Callhen	0.5734	0.5838	0.6387	0.4649	0.6848	0.5812
9	Chrys	0.5504	0.5508	0.6944	0.5217	0.6534	0.6263
10	Indoch36/3/11a	0.5321	0.5022	0.6004	0.4838	0.5971	0.5225
11	Mell	0.6078	0.5374	0.5672	0.4755	0.6017	0.6344
12	Hemsley	0.6357	0.6226	0.5985	0.4954	0.6136	0.6381
13	Latif	0.4991	0.4908	0.6160	0.3475	0.4871	0.4852
14	Erian	0.5017	0.5070	0.5674	0.3160	0.4782	0.4635
15	Chin3/6/14b	0.4154	0.4985	0.5705	0.3402	0.4735	0.4827
16	Chin460.4	0.4333	0.5166	0.6072	0.3325	0.4868	0.5025
17	Chin460.9	0.4275	0.5095	0.5934	0.3296	0.4830	0.4939
18	AdelBruno	0.4264	0.5298	0.5588	0.3167	0.4403	0.4513
19	AdelHay	0.3948	0.5120	0.5822	0.3093	0.4452	0.4565
20	AdelMatua	0.4386	0.5159	0.5986	0.3422	0.4762	0.4879
21	AdelChlorocarpa	0.4638	0.5844	0.5614	0.3073	0.5187	0.5287

	OTU no. ->	7	8	9	10	11	12
1	Argarg						
2	Argcord						
3	Rufa						
4	Melan						
5	Kolom						
6	Polyg3/12/11						
7	Valv						
8	Callhen	0.6336					
9	Chrys	0.7036	0.6768				
10	Indoch36/3/11a	0.5939	0.6469	0.8311			
11	Mell	0.6136	0.5824	0.6899	0.6268		
12	Hemsley	0.6793	0.6108	0.6735	0.5609	0.6363	
13	Latif	0.5016	0.4966	0.4709	0.4874	0.4535	0.5316
14	Erian	0.4673	0.4344	0.4076	0.3826	0.4440	0.5045
15	Chin3/6/14b	0.4541	0.4773	0.4680	0.4360	0.4053	0.5536
16	Chin460.4	0.4718	0.4875	0.4887	0.4622	0.4115	0.5809
17	Chin460.9	0.4725	0.5083	0.4858	0.4811	0.3876	0.5609
18	AdelBruno	0.4555	0.4240	0.4551	0.4381	0.3877	0.5453
19	AdelHay	0.4329	0.4428	0.4780	0.4515	0.4141	0.5099
20	AdelMatua	0.4714	0.4699	0.4914	0.4530	0.4267	0.5332
21	AdelChlorocarpa	0.5119	0.4513	0.4594	0.4119	0.4352	0.5653

	OTU no. ->	13	14	15	16	17	18
1	Argarg						
2	Argcord						
3	Rufa						
4	Melan						
5	Kolom						
6	Polyg3/12/11						
7	Valv						
8	Callhen						
9	Chrys						
10	Indoch36/3/11a						
11	Mell						
12	Hemsley						
13	Latif						
14	Erian	0.7671					
15	Chin3/6/14b	0.6884	0.7130				
16	Chin460.4	0.7073	0.7284	0.9336			
17	Chin460.9	0.7050	0.7070	0.9192	0.9305		
18	AdelBruno	0.6482	0.6778	0.8145	0.8404	0.8002	
19	AdelHay	0.6482	0.6535	0.8082	0.8434	0.8038	0.9017
20	AdelMatua	0.6929	0.6856	0.8227	0.8589	0.8213	0.8874
21	AdelChlorocarpa	0.6191	0.7049	0.8100	0.8397	0.8210	0.8643

	OTU no. ->	19	20	21
1	Argarg			
2	Argcord			
3	Rufa			
4	Melan			
5	Kolom			
6	Polyg3/12/11			
7	Valv			
8	Callhen			
9	Chrys			
10	Indoch36/3/11a			
11	Mell			
12	Hemsley			
13	Latif			
14	Erian			
15	Chin3/6/14b			
16	Chin460.4			
17	Chin460.9			
18	AdelBruno			
19	AdelHay			
20	AdelMatua	0.9003		
21	AdelChlorocarpa	0.8263	0.8461	

Table A4.2 PEARSON CORRELATION MATRIX

	YR2CC	YR1CC	YR2TX	YR1CAN	YR1PROF
YR2CC	1.000				
YR1CC	0.007	1.000			
YR2TX	-0.160	0.267	1.000		
YR1CAN	-0.004	0.076	-0.400	1.000	
YR1PROF	0.087	-0.139	0.355	0.072	1.000
YR1LEN	0.040	0.454	0.705	0.033	0.341
LFDR	0.275	0.462	0.181	-0.115	0.298
PETCDR	0.064	0.389	0.330	-0.061	0.091
APLAN	0.164	0.427	0.392	0.176	0.583
LEFAT	-0.135	-0.633	-0.575	0.129	-0.194
FRSHP	-0.055	0.674	0.132	0.281	0.079
JUVSHP	-0.154	0.333	0.463	0.224	0.476
JUVCOL	-0.031	-0.326	0.013	-0.180	-0.045
BASFRE	-0.067	-0.097	-0.365	-0.276	-0.493
LAMAR	0.125	0.708	0.635	-0.134	0.027
LLLW	-0.091	-0.369	-0.189	-0.229	-0.450
LAMW	0.146	0.647	0.577	-0.003	0.198
PETLE	-0.018	0.595	0.433	-0.068	0.089
FREAPT	-0.123	0.626	0.733	-0.020	0.208
SWT	0.223	-0.109	0.224	0.370	0.010
WTWAT	0.155	0.647	0.619	-0.039	0.105
VENTY	0.023	0.716	0.557	0.029	0.032
THLW	0.086	0.330	-0.042	0.374	-0.280
AOD	-0.007	0.527	0.356	0.123	0.139
TH2V1V	0.099	0.392	0.236	0.016	0.141
ARPUR	-0.007	0.718	0.232	0.223	-0.085
ARSIZ	0.023	-0.440	-0.323	-0.072	0.032
FREMAR	0.020	0.421	0.581	-0.297	-0.290
MAROR	-0.113	0.491	0.571	-0.032	0.216
TEEOR	0.023	0.716	0.557	0.029	0.032
PRVEIN	0.164	0.427	0.392	0.176	0.309
LFGLOS	-0.064	0.019	0.025	-0.010	-0.251
LFCOL	-0.179	-0.073	-0.207	0.127	-0.057
DISURHA	0.038	-0.355	-0.165	-0.327	-0.252
HAIRAB	0.214	0.685	0.512	-0.250	-0.098
ADSETHA	-0.023	0.055	-0.054	-0.230	0.194
NOPELAY	-0.148	0.437	0.084	0.356	0.138
PELTHLTH	0.225	0.596	0.538	-0.098	0.163
PRVINTH	0.448	0.481	0.374	-0.265	0.055
LAMHOR	-0.038	0.355	0.421	0.020	0.022
SHAPPBU	-0.287	0.374	0.488	0.232	0.164
PHENAB	-0.125	-0.423	-0.166	0.114	-0.072
TYCRYS	-0.447	-0.116	0.068	0.371	0.202
SPONSHP	0.172	-0.454	-0.178	-0.077	-0.146
ABAXPR	0.076	0.373	0.487	0.049	0.109
STOMPR	0.007	0.618	0.641	-0.024	0.085
ADAXCOL	-0.383	0.117	0.241	0.366	0.251
NOSCLLAY	-0.074	0.499	0.328	0.019	-0.223
INTERHYP	0.332	0.235	-0.376	0.111	-0.400
WAXFL	-0.271	-0.533	-0.063	0.044	-0.212
PITHSOL	-0.216	-0.364	-0.142	0.190	0.213
SETSPHA	-0.035	-0.213	-0.376	0.345	0.125
SIMABHIS	0.076	-0.023	0.181	0.012	0.238
SIMABSET	0.221	-0.270	-0.264	-0.176	-0.079
ABAXBIF	0.215	0.015	0.091	-0.178	0.181
ABAXNST	-0.271	-0.085	-0.063	-0.072	-0.212
ABAXST	0.055	0.539	0.660	0.141	0.395
BUDC	0.354	0.608	0.337	0.037	0.065
BCH	0.291	0.569	0.571	-0.214	-0.007
BCW	0.444	0.467	0.339	-0.239	0.039
OW	-0.261	0.228	0.168	-0.164	-0.072
CD	0.442	0.335	0.045	-0.024	-0.052
HTV	-0.338	0.056	0.047	0.021	-0.095
NOV	-0.056	0.201	0.089	-0.265	-0.129
LPD	-0.160	0.313	0.480	0.280	0.122
OL	0.045	0.483	0.356	-0.398	-0.200
BTO	0.343	0.617	0.493	-0.102	-0.005
DPET	-0.236	0.261	0.418	-0.061	-0.125
LENF	-0.194	0.221	0.134	0.174	-0.048
LEND	0.014	-0.162	-0.365	-0.095	-0.297
LENL	0.185	0.138	-0.081	0.037	-0.199
CANH	-0.305	0.296	0.443	-0.363	-0.232
BLBH	-0.396	-0.216	-0.118	0.370	0.129
BCOW	0.049	-0.086	-0.455	0.407	0.005
BCCD	0.126	0.467	0.585	-0.321	0.026
NVOW	-0.148	-0.020	-0.375	0.203	-0.297
BTBL	-0.395	-0.210	-0.065	0.321	0.113
DPBH	-0.241	0.040	0.180	-0.173	-0.128
STEMC	0.012	0.386	0.471	0.004	-0.015
NSHT	0.070	-0.148	-0.058	-0.205	0.087

	YR1LEN	LFOR	PETCOR	APLAN	LEFAT
YR1LEN	1.000				
LFOR	0.270	1.000			
PETCOR	0.338	0.495	1.000		
APLAN	0.661	0.462	0.117	1.000	
LEFAT	-0.508	-0.560	-0.196	-0.633	1.000
FRSHP	0.475	0.429	0.577	0.472	-0.408
JUVSHP	0.634	0.477	0.311	0.587	-0.532
JUVCOL	-0.021	-0.244	-0.301	0.077	0.232
BASFRE	-0.694	-0.289	-0.159	-0.722	0.338
.LAMAR	0.750	0.503	0.483	0.425	-0.694
LLLW	-0.480	-0.706	-0.146	-0.485	0.476
LAMW	0.794	0.610	0.445	0.496	-0.671
PETLE	0.631	0.446	0.447	0.404	-0.471
FREAPT	0.842	0.381	0.320	0.626	-0.679
SWT	0.287	-0.465	-0.243	0.074	-0.003
WTWAT	0.778	0.376	0.392	0.501	-0.629
VENTY	0.746	0.420	0.354	0.523	-0.750
THLW	0.006	-0.108	-0.122	0.085	-0.095
AOD	0.582	0.509	0.428	0.527	-0.523
TH2V1V	0.409	0.767	0.645	0.181	-0.304
ARPUR	0.582	0.509	0.428	0.527	-0.523
ARSIZ	-0.508	-0.315	0.079	-0.440	0.611
FREMAR	0.550	0.031	0.212	0.272	-0.524
MAROR	0.624	0.488	0.219	0.491	-0.789
TEEOR	0.746	0.420	0.354	0.523	-0.750
PRVEIN	0.661	-0.023	-0.156	0.618	-0.440
LFGLOS	-0.042	-0.149	-0.417	0.019	-0.216
LFCOL	-0.304	0.124	-0.139	0.097	-0.049
DISURHA	-0.223	0.131	0.320	-0.355	0.510
HAIRAB	0.572	0.520	0.401	0.582	-0.746
ADSETHA	-0.015	0.315	0.471	0.055	0.167
NOPELAY	0.185	0.176	-0.091	0.437	-0.484
PELTHLTH	0.559	0.536	0.313	0.499	-0.780
PRVINTH	0.348	0.392	0.418	0.297	-0.610
LAMHOR	0.436	0.119	-0.040	0.159	-0.510
SHAPPBU	0.431	0.059	0.400	0.210	-0.519
PHENAB	-0.367	-0.567	-0.599	-0.423	0.236
TYCRYS	-0.031	-0.361	0.187	-0.070	0.112
SPONSHP	-0.176	-0.152	-0.450	-0.253	0.347
ABAXPR	0.606	118	-0.133	0.373	-0.564
STOMPR	0.661	0.462	0.389	0.427	-0.826
ADAXCOL	0.264	-0.025	0.417	0.117	-0.196
NOSCLLAY	0.349	0.307	-0.061	0.380	-0.713
INTERHYP	-0.185	0.108	0.091	-0.213	-0.194
WAXFL	-0.341	-0.868	-0.411	-0.533	0.420
PITHSOL	-0.212	-0.301	0.156	-0.364	0.440
SETSPHA	-0.185	0.108	0.091	0.235	0.258
SIMABHIS	0.270	0.382	-0.198	0.220	-0.315
SIMABSET	-0.146	0.086	0.289	-0.067	0.408
ABAXBIF	-0.268	0.157	0.132	0.015	-0.281
ABAXNST	-0.462	-0.014	-0.091	-0.309	-0.258
ABAXST	-0.951	0.343	0.289	0.742	-0.612
BUDC	0.472	0.601	0.331	0.514	-0.583
BCH	0.603	0.460	0.172	0.493	-0.744
BCW	0.452	0.644	0.236	0.447	-0.541
OW	-0.007	-0.233	-0.110	0.008	-0.350
CD	0.177	0.498	0.315	0.313	-0.414
HTV	-0.053	-0.401	-0.140	-0.096	-0.132
NOV	0.056	-0.081	-0.508	0.136	-0.391
LPD	0.488	-0.132	0.445	0.242	-0.338
OL	0.325	0.148	-0.036	0.268	-0.647
BTO	0.476	0.478	0.391	0.411	-0.622
DPET	0.357	-0.239	0.448	-0.027	-0.096
LENF	0.119	0.310	0.143	0.225	-0.201
LEND	-0.312	0.191	-0.231	-0.010	0.186
LENL	0.086	0.083	-0.076	-0.103	-0.227
CANH	-0.045	0.221	0.209	-0.095	-0.422
BLBH	-0.203	-0.446	0.109	-0.222	0.287
BCOW	-0.172	0.243	0.215	0.113	0.378
BCCD	0.591	0.362	-0.012	0.445	-0.613
NVOW	-0.249	-0.181	-0.281	-0.373	0.367
BTBL	-0.182	-0.468	0.103	-0.222	0.251
DPBH	0.154	-0.241	0.428	-0.251	0.250
STEMC	0.522	0.385	0.256	0.241	-0.438
NSHT	-0.129	0.222	-0.546	0.279	-0.251

	FRSHP	JUVSHP	JUVCOL	BASFRE	LAMAR
FRSHP	1.000				
JUVSHP	0.494	1.000			
JUVCOL	-0.427	-0.064	1.000		
BASFRE	-0.193	-0.605	-0.142	1.000	
LAMAR	0.587	0.459	-0.328	-0.246	1.000
LLLW	-0.397	-0.677	0.409	0.439	-0.502
LAMW	0.584	0.597	-0.358	-0.385	0.944
PETLE	0.610	0.577	-0.337	-0.239	0.725
FREAPT	0.555	0.666	-0.296	-0.498	0.817
SWT	-0.214	-0.110	0.111	-0.202	0.120
WTWAT	0.490	0.496	-0.193	-0.389	0.890
VENTY	0.612	0.623	-0.446	-0.372	0.851
THLW	0.162	-0.136	-0.006	0.082	0.116
AOD	0.539	0.557	-0.480	-0.450	0.611
TH2V1V	0.447	0.482	-0.467	-0.247	0.592
ARPUR	0.742	0.557	-0.346	-0.294	0.698
ARSIZ	-0.204	-0.532	0.232	0.496	-0.495
FREMAR	0.341	0.165	-0.209	-0.111	0.685
MAROR	0.455	0.807	-0.259	-0.421	0.675
TEEOR	0.612	0.623	-0.446	-0.372	0.851
PRVEIN	0.270	0.206	-0.192	-0.488	0.456
LFGLOS	-0.433	-0.220	0.205	-0.064	-0.019
LFCOL	-0.181	0.032	0.309	-0.040	-0.308
DISURHA	-0.069	-0.249	0.118	0.226	-0.124
HAIRAB	0.402	0.263	-0.052	-0.323	0.734
ADSETHA	0.408	0.147	-0.232	-0.023	0.004
NOPELAY	0.316	0.369	-0.270	-0.179	0.204
PELTHLTH	0.391	0.360	-0.496	-0.236	0.773
PRVINTH	0.367	-0.050	-0.350	-0.095	0.624
LAMHOR	0.069	0.249	-0.533	-0.226	0.519
SHAPPBU	0.520	0.669	-0.427	-0.220	0.453
PHENAB	-0.555	-0.459	-0.089	0.285	-0.388
TYCRYS	0.275	0.373	-0.124	-0.028	-0.202
SPONSHP	-0.567	-0.385	0.505	0.145	-0.229
ABAXPR	0.099	0.248	-0.328	-0.343	0.594
STOMPR	0.472	0.587	-0.461	-0.331	0.827
ADAXCOL	0.577	0.583	-0.397	-0.159	0.198
NOSCLLAY	0.273	0.444	-0.264	-0.204	0.521
INTERHYP	0.158	-0.071	-0.360	0.271	0.116
WAXFL	-0.553	-0.476	0.203	0.310	-0.483
PITHSOL	0.067	0.133	-0.077	0.149	-0.340
SETSPHA	0.158	-0.071	-0.045	-0.096	-0.300
SIMABHIS	-0.086	0.316	-0.415	-0.289	0.273
SIMABSET	0.071	-0.359	0.285	0.028	-0.185
ABAXBIF	-0.115	-0.319	-0.065	0.127	-0.061
ABAXNST	-0.079	0.121	-0.113	0.402	-0.158
ABAXST	0.500	0.718	-0.142	-0.718	0.734
BUDC	0.364	0.141	-0.307	-0.224	0.712
BCH	0.246	0.260	-0.168	-0.240	0.770
BCW	0.255	0.151	-0.139	-0.141	0.671
OW	0.142	0.217	-0.144	0.141	0.046
CD	0.338	-0.047	-0.204	0.030	0.450
HTV	0.060	0.203	-0.073	0.077	-0.123
NOV	-0.185	0.019	0.013	-0.058	0.041
LPD	0.545	0.514	-0.147	-0.194	0.428
OL	0.149	0.152	-0.146	-0.086	0.460
BTO	0.298	0.078	-0.222	-0.167	0.773
DPET	0.239	0.154	0.032	0.031	0.402
LENF	0.202	0.113	-0.115	-0.149	0.320
LEND	-0.137	-0.051	0.520	0.157	-0.247
LENL	-0.072	-0.056	-0.269	-0.094	0.120
CANH	0.139	0.013	-0.370	0.343	0.399
BLBH	0.172	0.210	-0.060	0.093	-0.361
BCOW	0.203	-0.032	0.073	-0.034	-0.232
BCCD	0.041	0.245	-0.045	-0.333	0.616
NVOW	-0.237	-0.112	0.221	0.082	-0.303
BTBL	0.151	0.217	-0.035	0.095	-0.340
DPBH	0.096	-0.075	0.133	0.157	0.186
STEMC	0.393	0.366	-0.431	-0.187	0.706
NSHT	-0.342	0.158	0.570	-0.114	-0.179

	LLLW	LAMW	PETLE	FREAPT	SWT
LLLW	1.000				
LAMW	-0.722	1.000			
PETLE	-0.585	0.752	1.000		
FREAPT	-0.570	0.826	0.755	1.000	
SWT	0.159	0.098	-0.226	0.120	1.000
WTWAT	-0.448	0.811	0.626	0.783	0.246
VENTY	-0.580	0.850	0.730	0.906	0.083
THLW	0.112	0.030	-0.065	0.155	0.320
AOD	-0.619	0.670	0.596	0.748	-0.090
TH2V1V	-0.752	0.717	0.637	0.496	-0.290
ARPUR	-0.611	0.732	0.764	0.748	-0.093
ARSIZ	0.528	-0.548	-0.396	-0.679	-0.037
FREMAR	-0.029	0.537	0.460	0.712	0.231
MAROR	-0.624	0.726	0.544	0.757	-0.076
TEEOR	-0.580	0.850	0.730	0.906	0.083
PRVEIN	-0.328	0.480	0.371	0.626	0.443
LFGLOS	0.052	-0.031	-0.309	-0.040	0.325
LFCOL	-0.043	-0.264	-0.150	-0.200	-0.224
DISURHA	0.180	-0.146	-0.052	-0.212	-0.329
HAIRAB	-0.259	0.646	0.468	0.649	0.011
ADSETHA	-0.108	0.013	0.387	0.085	-0.634
NOPELAY	-0.401	0.263	0.317	0.406	0.022
PELTHLTH	-0.600	0.783	0.627	0.730	0.120
PRVINTH	-0.087	0.525	0.150	0.330	0.154
LAMHOR	-0.509	0.561	0.414	0.615	0.240
SHAPPBU	-0.282	0.443	0.499	0.576	0.088
PHENAB	0.181	-0.373	-0.331	-0.348	0.375
TYCRYS	0.175	-0.213	0.031	0.018	0.016
SPONSHP	0.104	-0.176	-0.356	-0.374	0.301
ABAXPR	-0.538	0.645	0.487	0.671	0.413
STOMPR	-0.596	0.834	0.692	0.823	0.105
ADAXCOL	-0.187	0.220	0.333	0.320	-0.023
NOSCLLAY	-0.441	0.502	0.542	0.668	0.004
INTERHYP	-0.048	0.093	-0.025	-0.175	-0.080
WAXFL	0.626	-0.572	-0.448	-0.439	0.456
PITHSOL	0.232	-0.315	-0.163	-0.299	-0.084
SETSPHA	-0.073	-0.229	-0.058	-0.175	-0.143
SIMABHIS	-0.729	0.445	0.251	0.381	0.029
SIMABSET	0.304	-0.218	-0.223	-0.347	-0.238
ABAXBIF	0.197	-0.134	-0.221	-0.255	-0.019
ABAXNST	0.122	-0.219	-0.170	-0.208	-0.238
ABAXST	-0.614	0.808	0.693	0.901	0.252
BUDC	-0.494	0.699	0.444	0.566	0.155
BCH	-0.425	0.741	0.420	0.688	0.259
BCW	-0.490	0.693	0.433	0.498	0.072
OW	0.153	-0.050	0.191	0.135	-0.122
CD	-0.282	0.419	0.230	0.166	0.042
HTV	0.223	-0.187	0.146	0.013	-0.076
NOV	-0.078	0.031	0.143	0.155	-0.031
LPD	0.029	0.358	0.315	0.467	0.356
OL	-0.123	0.380	0.455	0.438	-0.077
BTO	-0.266	0.682	0.306	0.540	0.331
DPET	0.271	0.229	0.271	0.246	0.183
LENF	-0.275	0.345	0.059	0.294	0.223
LEND	0.010	-0.224	-0.147	-0.236	-0.332
LENL	-0.255	0.189	0.082	0.016	0.142
CANH	-0.039	0.246	0.301	0.380	-0.188
BLBH	0.306	-0.378	-0.126	-0.197	-0.021
BCOW	-0.163	-0.131	0.012	-0.187	-0.216
BCCD	-0.408	0.634	0.371	0.678	0.186
NVOW	0.030	-0.236	-0.123	-0.255	-0.095
BTBL	0.338	-0.372	-0.138	-0.177	0.008
DPBH	0.344	0.044	0.174	-0.059	-0.056
STEMC	-0.466	0.717	0.431	0.717	0.172
NSHT	-0.108	-0.127	-0.252	-0.122	-0.153

	WTWAT	VENTY	THLW	AOD	TH2V1V
WTWAT	1.000				
VENTY	0.791	1.000			
THLW	0.125	0.062	1.000		
AOD	0.575	0.826	-0.061	1.000	
TH2V1V	0.470	0.548	-0.190	0.663	1.0
ARPUR	0.645	0.826	0.130	0.809	0.6
ARSIZ	-0.487	-0.750	-0.117	-0.716	-0.3
FREMAR	0.597	0.749	0.172	0.544	0.1
MAROR	0.616	0.836	-0.099	0.690	0.4
TEEOR	0.791	1.000	0.062	0.826	0.5
PRVEIN	0.519	0.523	0.338	0.336	-0.0
LFGLOS	-0.005	0.059	0.088	0.117	-0.1
LFCOL	-0.252	-0.221	0.111	0.073	-0.0
DISURHA	-0.242	-0.283	-0.135	-0.037	0.2
HAIRAB	0.672	0.716	0.132	0.661	0.3
ADSETHA	-0.035	-0.028	-0.207	0.138	0.3
NOPELAY	0.208	0.420	0.243	0.235	0.1
PELTHLTH	0.697	0.806	-0.014	0.665	0.5
PRVINTH	0.495	0.463	0.062	0.302	0.2
LAMHOR	0.481	0.679	0.095	0.626	0.3
SHAPPBU	0.451	0.636	-0.008	0.444	0.2
PHENAB	-0.343	-0.384	0.106	-0.465	-0.3
TYCRYS	-0.122	-0.026	-0.015	-0.068	-0.2
SPONSHP	-0.240	-0.463	0.061	-0.550	-0.1
ABAXPR	0.590	0.658	0.145	0.466	0.3
STOMPR	0.753	0.908	0.007	0.718	0.6
ADAXCOL	0.196	0.354	-0.140	0.292	0.1
NOSCLLAY	0.486	0.730	0.190	0.513	0.3
INTERHYP	0.052	0.258	-0.210	0.213	0.1
WAXFL	-0.383	-0.484	0.035	-0.586	-0.6
PITHSOL	-0.312	-0.330	-0.218	-0.400	-0.1
SETSPHA	-0.245	-0.194	-0.180	0.213	0.1
SIMABHIS	0.235	0.420	-0.293	0.509	0.4
SIMABSET	-0.262	-0.408	0.026	-0.135	-0.0
ABAXBIF	-0.113	-0.281	0.132	-0.340	-0.1
ABAXNST	-0.222	-0.032	-0.142	-0.139	-0.1
ABAXST	0.779	0.816	0.079	0.674	0.4
BUDC	0.650	0.588	0.284	0.549	0.5
BCH	0.705	0.761	0.110	0.623	0.4
BCW	0.553	0.550	-0.017	0.465	0.5
OW	0.075	0.263	-0.268	0.011	-0.3
CD	0.400	0.322	-0.017	0.324	0.4
HTV	-0.068	0.113	-0.260	-0.078	-0.3
NOV	0.074	0.218	-0.188	-0.017	-0.2
LPD	0.446	0.492	0.106	0.248	0.0
OL	0.394	0.577	-0.236	0.337	0.0
BTO	0.729	0.579	0.245	0.447	0.4
DPET	0.443	0.313	-0.133	0.198	0.0
LENF	0.236	0.234	0.078	0.349	0.3
LEND	-0.266	-0.268	0.145	-0.097	-0.0
LENL	0.155	0.220	-0.255	0.058	0.2
CANH	0.249	0.324	0.234	0.223	0.2
BLBH	-0.280	-0.221	-0.009	-0.253	-0.3
BCOW	-0.211	-0.236	0.115	0.164	0.3
BCCD	0.539	0.663	0.052	0.586	0.3
NVOW	-0.275	-0.323	0.394	-0.343	-0.1
BTBL	-0.255	-0.191	-0.025	-0.241	-0.3
DPBH	0.185	-0.037	-0.266	-0.053	0.0
STEMC	0.538	0.692	0.248	0.518	0.5
NSHT	-0.142	-0.135	-0.096	-0.163	-0.2

	ARPUR	ARSIZ	FREMAR	MAROR	TEEOR
ARPUR	1.000				
ARSIZ	-0.523	1.000			
FREMAR	0.544	-0.524	1.000		
MAROR	0.583	-0.789	0.501	1.000	
TEEOR	0.826	-0.750	0.749	0.836	1.000
PRVEIN	0.336	-0.440	0.421	0.276	0.523
LFGLOS	-0.019	-0.354	0.159	0.088	0.059
LFCOL	0.073	-0.049	-0.265	-0.041	-0.221
DISURHA	-0.037	0.311	0.025	-0.347	-0.283
HAIRAB	0.661	-0.537	0.698	0.541	0.716
ADSETHA	0.138	0.167	-0.075	-0.077	-0.028
NOPELAY	0.458	-0.258	0.145	0.288	0.420
PELTHLTH	0.685	-0.467	0.588	0.586	0.806
PRVINTH	0.232	-0.176	0.501	0.299	0.463
LAMHOR	0.430	-0.708	0.509	0.568	0.679
SHAPPBU	0.444	-0.354	0.381	0.670	0.636
PHENAB	-0.465	0.236	-0.248	-0.378	-0.384
TYCRYS	-0.068	0.159	-0.119	0.107	-0.026
SPONSHP	-0.349	0.347	-0.260	-0.443	-0.463
ABAXPR	0.466	-0.564	0.507	0.471	0.658
STOMPR	0.718	-0.633	0.643	0.813	0.908
ADAXCOL	0.292	-0.059	0.106	0.449	0.354
NOSCLLAY	0.633	-0.713	0.594	0.660	0.730
INTERHYP	0.213	-0.194	0.116	0.216	0.258
WAXFL	-0.586	0.420	-0.145	-0.467	-0.484
PITHSOL	-0.400	0.440	-0.396	-0.169	-0.330
SETSPHA	0.213	0.258	-0.232	-0.288	-0.194
SIMABHIS	0.266	-0.560	0.126	0.488	0.420
SIMABSET	-0.135	0.408	-0.105	-0.455	-0.408
ABAXBIF	-0.340	0.375	-0.210	-0.235	-0.281
ABAXNST	-0.139	-0.032	-0.058	0.288	-0.032
ABAXST	0.674	-0.612	0.524	0.682	0.816
BUDC	0.628	-0.317	0.430	0.301	0.588
BCH	0.599	-0.578	0.695	0.604	0.761
BCW	0.561	-0.292	0.453	0.349	0.550
OW	0.000	-0.208	0.201	0.379	0.263
CD	0.490	0.043	0.258	0.117	0.322
HTV	-0.095	-0.135	0.046	0.248	0.113
NOV	-0.020	-0.430	0.158	0.285	0.218
LPD	0.335	-0.093	0.421	0.440	0.492
OL	0.323	-0.532	0.545	0.525	0.577
BTD	0.478	-0.280	0.534	0.328	0.579
DPET	0.184	0.013	0.373	0.209	0.313
LENF	0.377	-0.181	0.198	0.165	0.234
LEND	0.098	0.032	-0.123	-0.149	-0.268
LENL	0.141	-0.165	0.027	0.132	0.220
CANH	0.223	-0.176	0.457	0.302	0.324
BLBH	-0.237	0.296	-0.269	-0.075	-0.221
BCOW	0.300	0.285	-0.328	-0.351	-0.236
BCCD	0.447	-0.703	0.617	0.577	0.663
NVOW	-0.191	-0.019	-0.391	-0.257	-0.323
BTBL	-0.245	0.263	-0.215	-0.034	-0.191
DPBH	-0.053	0.295	0.056	-0.108	-0.037
STEMC	0.518	-0.510	0.627	0.547	0.692
NSHT	-0.163	-0.251	-0.162	0.215	-0.135

	PRVEIN	LFGLOS	LFCOL	DISURHA	HAIRAB
PRVEIN	1.000				
LFGLOS	0.156	1.000			
LFCOL	-0.243	0.504	1.000		
DISURHA	-0.552	-0.320	-0.025	1.000	
HAIRAB	0.375	0.338	0.119	-0.096	1.000
ADSETHA	-0.138	-0.746	-0.123	0.481	-0.090
NOPELAY	0.437	0.091	0.057	-0.515	0.179
PELTHLTH	0.499	0.158	-0.126	-0.288	0.714
PRVINTH	0.363	0.111	-0.309	-0.160	0.661
LAMHOR	0.552	0.460	0.025	-0.394	0.416
SHAPPBU	0.210	-0.167	-0.104	-0.432	0.190
PHENAB	0.124	0.355	0.131	-0.348	-0.485
TYCRYS	-0.116	-0.416	-0.035	-0.219	-0.416
SPONSHP	-0.153	0.235	0.013	0.246	-0.259
ABAXPR	0.745	0.399	-0.083	-0.479	0.455
STOMPR	0.427	0.156	-0.073	-0.355	0.685
ADAXCOL	-0.019	-0.417	-0.139	-0.240	-0.116
NOSCLLAY	0.321	0.188	0.038	-0.312	0.523
INTERHYP	-0.213	0.228	-0.057	-0.175	0.185
WAXFL	-0.085	0.251	0.057	-0.208	-0.509
PITHSOL	-0.364	-0.701	-0.438	0.093	-0.720
SETSPHA	-0.213	-0.091	0.343	0.285	-0.058
SIMABHIS	0.220	0.198	-0.093	-0.119	0.125
SIMABSET	-0.270	-0.144	0.181	0.693	0.037
ABAXBIF	0.015	0.099	0.207	-0.255	0.092
ABAXNST	-0.533	0.091	0.257	-0.208	-0.145
ABAXST	0.742	0.000	-0.181	-0.347	0.585
BUDC	0.445	0.177	-0.055	-0.080	0.734
BCH	0.452	0.373	-0.073	-0.190	0.856
BCW	0.270	0.109	-0.164	0.091	0.706
OW	0.049	-0.071	-0.144	-0.545	0.011
CD	0.059	0.120	0.057	0.040	0.569
HTV	-0.013	-0.098	-0.081	-0.518	-0.189
NOV	0.305	0.282	-0.046	-0.556	0.144
LPD	0.213	-0.249	-0.286	-0.307	0.187
OL	0.317	0.239	-0.125	-0.420	0.574
BTO	0.391	0.230	-0.166	-0.121	0.781
DPET	0.005	0.014	-0.195	-0.116	0.273
LENF	0.019	0.249	0.201	0.151	0.315
LEND	-0.415	0.158	0.576	0.506	0.041
LENL	0.119	0.253	-0.120	-0.342	0.107
CANH	-0.095	-0.017	0.038	0.084	0.321
BLBH	-0.223	-0.444	-0.065	-0.154	-0.568
BCOW	-0.275	-0.136	0.463	0.484	-0.054
BCCD	0.498	0.463	-0.013	-0.166	0.751
NVOW	-0.053	0.096	0.285	0.015	-0.361
BTBL	-0.221	-0.404	-0.068	-0.174	-0.528
DPBH	-0.200	-0.125	-0.194	0.149	0.018
STEMC	0.313	-0.126	-0.482	0.125	0.401
NSHT	-0.148	0.323	0.341	-0.122	0.085

	ADSETHA	NOPELAY	PELTHLTH	PRVINTH	LAMHOR
ADSETHA	1.000				
NOPELAY	-0.194	1.000			
PELTHLTH	-0.120	0.497	1.000		
PRVINTH	-0.043	0.015	0.593	1.000	
LAMHOR	-0.283	0.285	0.667	0.284	1.000
SHAPPBU	0.024	0.411	0.413	0.152	0.432
PHENAB	-0.443	0.099	-0.108	-0.250	0.278
TYCRYS	0.211	0.156	-0.296	-0.320	-0.159
SPONSHP	-0.449	-0.129	-0.189	-0.248	-0.246
ABAXPR	-0.376	0.437	0.767	0.313	0.862
STOMPR	-0.138	0.437	0.887	0.492	0.748
ADAXCOL	0.196	0.228	0.119	-0.039	0.100
NOSCLLAY	-0.189	0.595	0.667	0.127	0.557
INTERHYP	-0.258	0.050	0.208	0.325	0.175
WAXFL	-0.420	-0.138	-0.390	-0.322	-0.022
PITHSOL	0.330	-0.139	-0.518	-0.337	-0.486
SETSPHA	0.194	0.050	-0.020	-0.257	-0.285
SIMABHIS	-0.175	0.176	0.536	0.026	0.618
SIMABSET	0.408	-0.553	-0.391	0.119	-0.485
ABAXBIF	-0.047	0.073	0.137	0.460	-0.080
ABAXNST	-0.194	0.125	-0.049	-0.098	-0.022
ABAXST	-0.000	0.395	0.658	0.311	0.555
BUDC	-0.154	0.381	0.823	0.575	0.415
BCH	-0.323	0.195	0.842	0.626	0.597
BCW	-0.100	0.161	0.772	0.550	0.280
OW	0.019	0.170	0.075	0.043	0.125
CD	-0.151	0.169	0.651	0.541	0.105
HTV	0.011	0.111	-0.126	-0.191	0.064
NOV	-0.195	0.186	0.217	0.043	0.332
LPD	-0.053	0.244	0.229	0.235	0.093
OL	-0.092	0.142	0.535	0.412	0.450
BTO	-0.232	0.181	0.760	0.757	0.372
DPET	-0.120	-0.099	0.112	0.170	0.070
LENF	-0.082	0.077	0.299	0.191	0.149
LEND	0.054	-0.108	-0.297	-0.383	-0.361
LENL	-0.320	0.188	0.404	0.220	0.389
CANH	0.067	0.139	0.427	0.205	0.323
BLBH	0.220	0.059	-0.486	-0.379	-0.314
BCOW	0.263	-0.014	-0.139	-0.343	-0.328
BCCD	-0.256	0.072	0.655	0.438	0.655
NVOW	0.022	-0.064	-0.494	-0.456	-0.016
BTBL	0.185	0.030	-0.473	-0.347	-0.290
DPBH	0.082	-0.345	-0.171	0.004	-0.175
STENC	-0.038	0.281	0.585	0.360	0.434
NSHT	-0.296	0.035	-0.113	-0.184	-0.198

	SHAPPBU	PHENAB	TYCRYS	SPONSHP	ABAXPR
SHAPPBU	1.000				
PHENAB	-0.084	1.000			
TYCRYS	0.689	0.027	1.000		
SPONSHP	-0.638	0.381	-0.531	1.000	
ABAXPR	0.319	0.333	-0.291	0.049	1.00
STOMPR	0.701	-0.150	-0.024	-0.354	0.74
ADAXCOL	0.867	-0.111	0.841	-0.593	-0.00
NOSCLLAY	0.452	-0.062	-0.103	-0.164	0.61
INTERHYP	0.164	-0.099	-0.102	-0.224	0.00
WAXFL	0.027	0.793	0.335	0.263	0.00
PITHSOL	0.280	-0.033	0.742	-0.182	-0.55
SETSPHA	-0.219	-0.099	0.005	0.011	-0.21
SIMABHIS	0.059	0.128	-0.361	0.103	0.59
SIMABSET	-0.520	-0.313	-0.227	0.142	-0.49
ABAXBIF	-0.040	0.321	-0.071	0.016	0.00
ABAXNST	0.411	0.152	0.389	-0.207	-0.21
ABAXST	0.520	-0.313	0.016	-0.284	0.69
BUDC	0.032	-0.231	-0.541	0.052	0.56
BCH	0.177	-0.245	-0.518	-0.024	0.68
BCW	-0.118	-0.347	-0.691	0.208	0.48
OW	0.555	0.043	0.478	-0.560	0.08
CD	-0.058	-0.161	-0.482	0.151	0.29
HTV	0.556	0.155	0.622	-0.512	-0.04
NOV	0.045	0.264	-0.203	-0.063	0.40
LPD	0.832	-0.243	0.695	-0.480	0.10
OL	0.281	-0.080	-0.221	-0.315	0.47
BTO	0.105	-0.268	-0.465	-0.014	0.49
DPET	0.477	-0.233	0.359	-0.350	0.00
LENF	0.004	-0.152	-0.186	0.058	0.16
LEND	-0.494	-0.238	-0.329	0.390	-0.34
LENL	0.093	0.351	-0.293	0.17	0.491
CANH	0.312	0.043	-0.006	-0.191	0.22
BLBH	0.525	0.064	0.968	-0.443	-0.45
BCOW	-0.324	-0.218	-0.094	0.150	-0.29
BCCD	0.044	-0.192	-0.560	-0.018	0.67
NVOW	-0.213	0.252	-0.001	0.201	-0.10
BTBL	0.550	0.052	0.969	-0.463	-0.44
DPBH	0.135	-0.183	0.222	-0.144	-0.22
STEMC	0.305	-0.301	-0.168	-0.029	0.46
NSHT	-0.350	-0.110	-0.348	0.353	-0.09

	STOMPR	ADAXCOL	NOSCLLAY	INTERHYP	WAXFL
STOMPR	1.000				
ADAXCOL	0.389	1.000			
NOSCLLAY	0.737	0.152	1.000		
INTERHYP	0.235	0.091	0.173	1.000	
WAXFL	-0.309	0.068	-0.266	-0.125	1.000
PITHSOL	-0.364	0.564	-0.420	-0.085	0.235
SETSPHA	-0.213	0.091	-0.106	-0.050	-0.125
SIMABHIS	0.462	-0.025	0.458	0.108	-0.298
SIMABSET	-0.472	-0.289	-0.589	-0.158	-0.158
ABAXBIF	0.015	-0.099	-0.154	-0.073	0.200
ABAXNST	0.139	0.388	0.293	0.400	0.213
ABAXST	0.742	0.289	0.484	-0.158	-0.395
BUDC	0.616	-0.186	0.463	0.076	-0.515
BCH	0.763	-0.144	0.600	0.200	-0.414
BCW	0.541	-0.307	0.442	0.143	-0.598
OW	0.248	0.454	0.328	0.303	0.199
CD	0.420	-0.091	0.265	0.368	-0.340
HTV	0.113	0.528	0.214	0.234	0.370
NOV	0.227	-0.168	0.502	0.154	0.087
LPD	0.463	0.784	0.183	0.078	0.093
OL	0.572	0.001	0.617	0.343	-0.136
BTO	0.615	-0.160	0.365	0.114	-0.392
DPET	0.288	0.418	-0.036	0.166	0.195
LENF	0.245	-0.014	0.210	-0.128	-0.271
LEND	-0.340	-0.441	0.026	-0.084	-0.263
LENL	0.380	-0.035	0.333	0.476	0.113
CANH	0.461	0.155	0.523	-0.115	-0.039
BLBH	-0.237	0.726	-0.269	-0.063	0.390
BCOW	-0.276	-0.070	-0.217	-0.123	-0.273
BCCD	0.620	-0.303	0.527	-0.004	-0.378
NVOW	-0.332	-0.278	-0.157	-0.170	0.153
BTBL	-0.209	0.727	-0.252	-0.041	0.408
DPBH	-0.048	0.220	-0.368	0.048	0.209
STEMC	0.602	0.149	0.560	-0.028	-0.453
NSHT	-0.148	-0.406	0.228	-0.035	-0.222

	PITHSOL	SETSPHA	SIMABHIS	SIMABSET	ABAXBIF
PITHSOL	1.000				
SETSPHA	-0.085	1.000			
SIMABHIS	-0.301	0.108	1.000		
SIMABSET	-0.067	0.316	-0.429	1.000	
ABAXBIF	-0.124	-0.073	-0.256	0.115	1.000
ABAXNST	0.235	-0.125	-0.014	-0.395	0.200
ABAXST	-0.270	-0.158	0.343	-0.286	-0.229
BUDC	-0.638	0.132	0.370	-0.070	0.177
BCH	-0.703	-0.138	0.463	-0.230	-0.013
BCW	-0.610	0.083	0.465	-0.030	0.005
OW	0.251	-0.307	-0.095	-0.572	0.003
CD	-0.513	0.400	0.228	0.135	0.272
HTV	0.388	-0.234	-0.163	-0.528	-0.066
NOV	-0.289	-0.312	0.299	-0.568	0.018
LPD	0.385	-0.178	-0.270	-0.274	-0.084
OL	-0.411	-0.294	0.248	-0.427	0.032
BTO	-0.553	-0.096	0.196	-0.088	0.255
DPET	0.157	-0.159	-0.318	-0.105	-0.129
LENF	-0.330	0.300	0.220	0.029	-0.037
LEND	-0.317	0.276	-0.114	0.434	-0.244
LENL	-0.235	-0.096	0.395	-0.386	0.119
CANH	-0.195	-0.115	0.151	-0.249	0.249
BLBH	0.827	-0.021	-0.472	-0.134	-0.056
BCOW	-0.125	0.805	-0.066	0.516	-0.143
BCCD	-0.724	-0.267	0.510	-0.231	-0.143
NVOW	0.038	-0.377	-0.258	0.057	-0.107
BTBL	0.809	-0.068	-0.477	-0.155	-0.062
DPBH	0.259	-0.086	-0.394	0.186	-0.092
STEMC	-0.125	-0.197	0.476	-0.241	-0.285
NSHT	-0.290	-0.035	0.222	-0.110	-0.050

	ABAXNST	ABAXST	BUDC	BCH	BCW
ABAXNST	1.000				
ABAXST	-0.395	1.000			
BUDC	-0.328	0.527	1.000		
BCH	-0.121	0.613	0.789	1.000	
BCW	-0.266	0.442	0.846	0.855	1.0
OW	0.576	0.043	-0.362	-0.020	-0.2
CD	-0.053	0.162	0.755	0.620	0.7
HTV	0.531	-0.014	-0.531	-0.253	-0.4
NOV	0.224	0.114	-0.078	0.247	0.1
LPD	0.196	0.473	0.015	0.144	-0.0
OL	0.207	0.343	0.220	0.569	0.3
BTO	-0.220	0.477	0.888	0.831	0.7
DPET	0.059	0.248	0.037	0.126	-0.0
LENF	-0.034	0.151	0.400	0.357	0.3
LEND	0.058	-0.300	-0.059	-0.064	0.1
LENL	0.103	0.099	0.190	0.296	0.2
CANH	0.430	-0.003	0.333	0.355	0.2
BLBH	0.375	-0.175	-0.666	-0.684	-0.7
BCOW	-0.291	-0.139	0.182	-0.181	0.0
BCCD	-0.236	0.605	0.575	0.883	0.6
NVOW	-0.107	-0.190	-0.357	-0.427	-0.4
BTBL	0.408	-0.163	-0.680	-0.639	-0.7
DPBH	-0.103	-0.016	-0.120	-0.174	-0.2
STEMC	-0.115	0.522	0.580	0.591	0.5
NSHT	0.278	-0.110	-0.070	0.146	0.1

	OW	CD	HTV	NOV	LPD
OW	1.000				
CD	-0.249	1.000			
HTV	0.933	-0.416	1.000		
NOV	0.652	-0.102	0.555	1.000	
LPD	0.415	-0.020	0.420	-0.191	1.0
OL	0.670	0.202	0.509	0.815	0.1
BTO	-0.191	0.666	-0.408	-0.034	0.1
DPET	0.326	0.017	0.363	-0.182	0.6
LENF	-0.264	0.287	-0.362	-0.133	0.0
LEND	-0.389	0.085	-0.403	-0.174	-0.4
LENL	0.168	0.372	0.133	0.508	-0.1
CANH	0.188	0.197	0.044	0.091	0.1
BLBH	0.431	-0.560	0.599	-0.238	0.5
BCOW	-0.629	0.326	-0.523	-0.586	-0.2
BCCD	-0.003	0.262	-0.195	0.412	-0.0
NVOW	-0.189	-0.553	-0.033	0.028	-0.3
BTBL	0.483	-0.568	0.635	-0.202	0.6
DPBH	0.102	-0.072	0.208	-0.300	0.3
STEMC	-0.172	0.226	-0.305	-0.094	0.2
NSHT	0.066	-0.005	-0.032	0.410	-0.3

	OL	BTO	DPET	LENF	LEND
OL	1.000				
BTO	0.318	1.000			
DPET	0.193	0.236	1.000		
LENF	-0.029	0.495	-0.070	1.000	
LEND	-0.261	-0.194	-0.381	0.189	1.000
LENL	0.447	0.167	-0.184	-0.042	-0.308
CANH	0.293	0.371	0.121	0.270	-0.046
BLBH	-0.325	-0.582	0.298	-0.281	-0.277
BCOW	-0.563	-0.089	-0.230	0.270	0.546
BCCD	0.601	0.621	-0.004	0.326	-0.018
NVOW	-0.287	-0.414	-0.315	-0.162	0.297
BTBL	-0.271	-0.560	0.339	-0.283	-0.288
DPBH	-0.019	0.007	0.863	-0.201	-0.259
STEMC	0.139	0.358	0.027	0.385	-0.139
NSHT	0.187	-0.090	-0.391	0.048	0.573

	LENL	CANH	BLBH	BCOW	BCCD
LENL	1.000				
CANH	-0.080	1.000			
BLBH	-0.321	-0.122	1.000		
BCOW	-0.231	-0.183	-0.079	1.000	
BCCD	0.215	0.264	-0.707	-0.276	1.000
NVOW	-0.013	-0.234	0.112	0.066	-0.176
BTBL	-0.317	-0.105	0.995	-0.143	-0.657
DPBH	-0.246	-0.026	0.248	-0.064	-0.229
STEMC	0.020	0.459	-0.291	-0.153	0.505
NSHT	-0.060	-0.080	-0.331	-0.087	0.248

	NVOW	BTBL	DPBH	STEMC	NSHT
NVOW	1.000				
BTBL	0.083	1.000			
DPBH	-0.125	0.259	1.000		
STEMC	-0.262	-0.289	-0.179	1.000	
NSHT	0.018	-0.306	-0.413	-0.113	1.000

NUMBER OF OBSERVATIONS: 21

Correlation coefficients > 0.67 are statistically significant at the 95% probability level.

APPENDIX 4.3

Page 1

Key to character codes in correlation matrix

Character states are described in Appendices 2 and 3

YR2CC	2 year cane colour
YR1CC	1 year cane colour
YR2TX	2 year cane texture
YR1CAN	1 year cane colour other than glaucous
YR1PROF	1 year cane lenticel profile
YR1LEN	1 year cane maximum internode length
LFOR	leaf form as a whole
PETCOR	petiole course
APLAN	leaf apex height in relation to the plane of cane
LEFAT	leaf flatness in the middle
FRSHP	frequency of mature leaf shape types
JUVSHP	juvenile leaf shape types
JUVCOL	juvenile shoot hair colour
BASFRE	frequency of leaf base types
LAMAR	lamina area (cm^2)
LLLW	leaf length to leaf width ratio
LAMW	lamina width (cm)
PETLE	petiole length (cm)
FREAPT	frequency of leaf apex types
SWT	specific leaf weight (mg/cm^2)
WTWAT	weight of water in leaf blade (g)
VENTY	type of leaf venation (= architecture)
THLW	vein thickness to lamina width ratio
AOD	variations in angle of divergence of 2° veins
TH2VTV	thickness of 2° vein c.f. 1° vein
ARPUR	areole perfection

App. 4.3 continued.

APPENDIX 4.3

Page 2

Key to character codes in correlation matrix

ARSIZ	maximum areole size (range)
FREMAR	frequency of margin types
MAROR	orientation of margin
TEEOR	orientation of marginal teeth
PRVEIN	principal vein of tooth
LFGLOS	leaf gloss adaxial surface
LFCOL	leaf colour adaxial surface
DISURHA	distribution of hairs on adaxial surface
HAIRAB	abundance of hairs on abaxial surface
ADSETHA	presence of adaxial setose hairs
NOPELAY	frequency of palisade layers
PELTHLTH	palisade thickness to leaf thickness ratio
PRVINTH	primary vein diameter to interveinal thickness ratio
LAMHOR	lamina horizon relative to height of 1° vein
SHAPPBU	shape of 1° bundle near petiole base (after Gao)
PHENAB	abundance of phenolics near 1° vein
TYCRYS	types of ergastic Ca crystals
SPONSHP	spongy mesophyll cell shape
ABAXPR	abaxial surface profile
STOMPR	stomatal protuberance
ADAXCOL	presence of adaxial collenchyma above minor bundles
NOSCLLAY	frequency of sclerenchyma layers in bundle
INTERHYP	presence of continuous interveinal hypoderm
WAXFL	presence of coarse flakes of epicuticular wax
PITHSOL	pith solidity (?)
SETSPHA	setose spiny hairs as a 2° development

App. 4.3 continued...

Key to character codes in correlation matrix

SIMABHIS	simple abaxial hairs hispid
SIMABSET	simple abaxial hairs setose or hirsute
ABAXBIF	abaxial hairs + bifids
ABAXNST	abaxial stellate hairs not obviously stalked
ABAXST	abaxial stellate hairs stalked
BUDC	bud-case length (mm)
B H	bud-case height (mm)
BCW	bud-case width (mm)
OW	ostiole width (mm)
CD	cane diameter (mm)
HTV	height of externally visible bud structures (mm)
NOV	no. of externally visible bud structures
LPD	length of petiole base scar (mm)
OL	ostiole length (mm)
BTO	base to highest point (bud summit) (mm)
DPET	depth of petiole scar (mm)
LENF	lenticel frequency side of bud-case
LEND	lenticel density ($.cm^{-2}$)
LENL	length of longest lenticel (mm)
CANH	cane hair base density ($.cm^{-2}$)
BLBH	bud-length to bud-case height ratio
BCOW	bud-case width to ostiole width ratio
BCCD	bud-case height to cane diameter ratio
NVOW	number of visible bud structures to ostiole width ratio
BTBL	bud-case height to bud-case length ratio
DPBH	depth of petiole scar to bud-case height ratio
STEMC	stem colour
NSHT	number of shoots per bud-case

APPENDIX 5

Conference Abstracts

(1) 2nd International Symposium on Kiwifruit,
18-21 February 1991, Palmerston North, N.Z.

(a) Oral presentation :

STRUCTURE OF THE KIWIFRUIT STEM

James M. Condon
Dept. of Plant and Microbial Sciences
University of Canterbury
Christchurch
New Zealand

The structure of the kiwifruit stem is not as anomalous as that of some tropical vines. Phloem has prominent raphides and sieve-tube elements with compound sieve-plates, like *Vitis*. The wood is semi ring-porous and axial parenchyma is abundant. Vessel-elements are up to 1 mm long and have end-walls with simple, scalariform, reticulate or "combination" perforation plates. Paint-infusion of 1-2 m long 'Hayward' trunks show that average vessel (conduit) length is 0.6 m with some vessels up to 1 m long.

(b) Poster presentation :

COMPARATIVE MORPHOLOGY AS AN AID TO *ACTINIDIA* TAXONOMY

James M. Condon
Dept. of Plant and Microbial Sciences
University of Canterbury
Christchurch
New Zealand

Examination of winter and summer shoots of 20-30 *Actinidia* taxa obtained from the DSIR *Actinidia* germplasm collection, confirmed the value of morphological characters in *Actinidia* taxonomy. Vegetative characters derived from summer and dormant winter shoots were used to produce computer-generated groupings, which mostly agree with existing taxonomy. Future use should be made of three-dimensional form and winter shoot characters in *Actinidia* taxonomy.

(2) 16th National Conference N.Z. Society for Electron Microscopy
20-24 May 1991, Wellington, N.Z.

Poster presentation :

STRUCTURE OF THE KIWIFRUIT STEM

James M. Condon
Dept. of Plant and Microbial Sciences
University of Canterbury
Christchurch
New Zealand

Actinidia deliciosa var. *deliciosa* cv. Hayward (kiwifruit) is a deciduous, rambling vine of horticultural importance.

Phloem is similar to that of the grape. Functional (actively conducting) sieve-elements are long-lived, with end-walls that terminate in scalariformly compound sieve-plates. Radial transport is interrupted by crushing and sclerification of outer phloem. Mucilaginous raphide cells are conspicuous amongs phloem and cortical tissies.

Xylem is a diverse tissue which comprises mostly fibre-tracheids, together with axial and radial parenchyma. Perforation plates of xylem vessels may be scalariform, reticulate or "combination" types, but simple (open-ended) plates are the most common. Vessels of kiwifruit stems are large (65-235 μm in diameter and up to 0.8 m long), mostly solitary and are surrounded by (living) parenchyma cells.

Rays are large, heterogeneous structures which commonly store starch and phenolic bodies during the winter.